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Amphibians of La Escalera Region, Southeastern Venezuela: Taxonomy, Ecology, and Biogeography

By

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ABSTRACT Data are presented on the characteristics and natural history of 57 species of anuran amphibians from a transect from El Dorado in humid tropical forest across the Sierra de Lema to the Gran Sabana, Estado de Bolívar, Venezuela. *Allophryne ruthveni*, *Phyllomedusa tomopterna*, and *Elachistocleis* sp. are reported for the first time from Venezuela. Descriptions and illustrations of tadpoles are presented for *Colostethus parkerae*, *Hyla multifasciata*, *Leptodactylus longirostris*, *L. rugosus*, and *L. sabanensis*. Descriptions and illustrations of advertisement calls are presented for *Bufo granulosus*, *Hyla lemai*, *H. minuscula*, *H. minuta*, *H. multifasciata*, *Phyllomedusa hypocondrialis*, *Leptodactylus rugosus*, *Physalaemus enesefae*, *Ctenophryne geayi*, and *Elachistocleis* sp. Analysis of utilization of calling sites by anurans in five communities shows greater overlap of calling sites with size of adult males in humid tropical forest than in very humid lower montane forest and grassland on the Gran Sabana. Few species are distributed throughout the elevational transect, but some species that occur in savannas in the lowlands also occur on the Gran Sabana. Comparison of the anuran faunas at 12 sites in the Guianan region reveals that the fauna in the humid tropical forest in the lowlands to the north of the Sierra de Lema contains a mixture of forest-dwelling and savanna-inhabiting species, and that the fauna in the very humid lower montane forest on the northern slopes of the Sierra de Lema is primarily a mixture of endemics and species shared with the Gran Sabana. Significant negative correlations between distances between sites and coefficients of biogeographic resemblance exist among sites in savannas, between sites in savannas and lowland rainforest, and between sites in savannas and cloud forest.

Key words: Anura, Venezuelan Guayana, Taxonomy, Natural history, Communities, Biogeography.

RESUMEN Se presentan datos sobre las características y la historia natural de 57 especies de anfibios anuros en un transecto desde El Dorado, en bosque tropical húmedo, a través de la Sierra de Lema, hasta la Gran Sabana, en el Estado de Bolívar, Venezuela. *Allophryne ruthveni*, *Phyllomedusa tomopterna* and *Elachistocleis* sp. se citan por primera vez para Venezuela. Se presentan descripciones e ilustraciones de los renacuajos de *Colostethus parkerae*, *Hyla multifasciata*, *Leptodactylus longirostris*, *L. rugosus*, y *L. sabanensis*. Se presentan descripciones e ilustraciones de las llamadas de advertencia de *Bufo granulosus*, *Hyla lemai*, *H. minuscula*, *H. minuta*, *H. multifasciata*, *Phyllomedusa hypocondrialis*, *Leptodactylus rugosus*, *Physalaemus enesefae*, *Ctenophryne geayi* and *Elachistocleis* sp. El análisis de la utilización de los lugares de llamada de los anuros en cinco comunidades demuestra que el solapamiento entre los lugares de llamada y el tamaño de los machos adultos es mayor en el bosque húmedo tropical que en el bosque muy húmedo montano bajo y en las pampas de la Gran Sabana. Pocas especies se distribuyen a través de todo el transecto altitudinal, pero algunas especies que se hallan en las sabanas de las tierras bajas también se encuentran en la Gran Sabana. La comparación de las faunas de anuros en 12 localidades de la región guayanesa revela que la fauna del bosque húmedo tropical de tierras bajas hasta el norte de la Sierra de Lema contiene una mezcla de especies de bosque y especies de sabana, y que la fauna del bosque muy húmedo montano bajo de las laderas norte de la Sierra de Lema es sobre todo una mezcla de endemismos y de especies compartidas con la Gran Sabana. Existe una correlación negativa significativa entre las distancias entre localidades y los coeficientes de semejanza biogeográfica entre localidades de sabanas, entre localidades de sabana y de bosque tropical de tierras bajas y entre localidades de sabana y de bosque de neblina.

Palabras claves: Anura, Guayana venezolana, Taxonomía, Historia natural, Comunidades, Biogeografía.

INTRODUCTION

The Venezuelan Guayana, comprising most of the Estado Bolívar, in the southeastern part of the country is renowned geographically for its isolated tabletop mountains (tepuyes or tepuis) and the spectacular Angel Falls. In recent years, the anurans of the tepuyes have received considerable attention (e.g., Ayarzagüena, 1992; Ayarzagüena et al., 1992a; Myers and Donnelly, 1996, 1997; Señaris et al., 1994), whereas the biota of the surrounding lower elevations has been largely neglected.

In August 1965, members of an expedition sponsored by the Museo de Biología of the Universidad Central de Venezuela collected a few amphibians in the lowland tropi-

cal rainforest south of El Dorado and on the lower slopes of the Sierra de Lema in southeastern Venezuela (Heatwole et al., 1965). In March 1968, Juan A. Rivero collected briefly on the north slope of the Sierra de Lema. The steep ascent of this range, which forms the northern edge of the elevated Gran Sabana, is known locally as La Escalera. Subsequent to his visit there, Rivero (1968a, b; 1970; 1971b) described five new species of anurans from La Escalera.

In July 1974, Dana Trueb Duellman, Juan R. León, John E. Simmons, Linda Trueb, and I made herpetological collections from the lowlands, across the Sierra de Lema, and onto the Gran Sabana. This same transect was repeated by

Marinus S. Hoogmoed in May and June 1978. In January 1979, accompanied by Stefan Gorzula and Glenda Medina-Cuervo, I again worked on the north slope of the Sierra de Lema and on the Gran Sabana in the vicinity of Cabanayén (Fig. 1). A few additional specimens of anurans were collected between El Dorado and the Gran Sabana by the late Scott J. Maness in March 1975, by John E. Cadle in December 1980, and by Robert H. Dean in February 1981.

The visit to this region in 1974 was a spectacular success. Traveling and living in a large, chassis-mounted camper, we were able to work (and live comfortably) wherever we could park the vehicle. Clearings for former road construction camps at Km 104 and 127 were especially convenient. Construction and military personnel extended various courtesies, not the least of which was replenishing our dwindling food supplies. We were fortunate to collect 46 of the 57 species now known from the area, and were able to obtain life history data and recordings of vocalizations of many species during the two weeks that we spent there. As fate would have it, at our last campsite at 13 km S and 1 km E of the Puente Cuyuni, we experienced a heavy rain that brought out thousands of frogs. Although we wanted to stay more than the one night, our food supplies and schedule would not permit our doing so.

Part of the long delay in reporting on this material resulted from having to solve numerous taxonomic problems. Among these the clarification of the status of *Hyla sibleszi* by Hoogmoed (1979a); review of the genus *Stefania* by Duellman and Hoogmoed (1984); description of two new species of *Ololygon* (= *Scinax*) by Duellman (1986); taxonomy of *Pipa* by Trueb and Cannatella (1986); status of the *Centrolenella* (= *Hyalinobatrachium*) by Cannatella and Lamar (1986); status of *Hyla* (= *Tepuihyla*) *rodriguezi* by Duellman and Hoogmoed (1992); taxonomy of frogs in the *Leptodactylus wagneri* complex by Heyer (1994); and description of a new species of *Colostethus* by Meinhardt and Parmelee (1996). Species from a lowland site (13 km S, 1 km E Puente Cuyuni) were included in analyses of anuran communities by Duellman (1988).

The purposes of this paper are to: (1) report the 57 species of anurans known from a transect between El Dorado

and the Gran Sabana; (2) provide accumulated information of the ecological distribution and reproductive behavior of these species, including descriptions of tadpoles and advertisement calls; (3) compare microhabitat utilization among species at sites in different macrohabitats; (4) analyze the geographical distribution of anurans along the transect with respect to major habitats; and (5) review the biogeography of the anuran fauna. By so doing, I hope to contribute to the meager knowledge of the structure, coloration in life, habitat, and behavior of many species of anurans in northeastern South America. Color photographs (Plates 1, 2) are provided of 16 species, descriptions and illustrations of tadpoles of six species, and descriptions of advertisement calls of 10 species.

ACKNOWLEDGMENTS

The acquisition of most of the material on which this paper is based was collected with the amiable assistance of Dana Trueb Duellman, Juan R. León, John E. Simmons, and Linda Trueb in 1974, and Stefan F. Gorzula and Glenda Medina-Cuervo in 1979; the field work was supported by a grant (DEB 7401998) from the National Science Foundation. I am especially grateful to Marinus S. Hoogmoed, who made available the specimens, and accompanying field notes, that he collected in 1978, and to Stefan Gorzula, who provided many maps and references. Also, for the loan of specimens, I thank James R. Dixon, Texas Cooperative Wildlife Collection; Juan A. Rivero, University of Puerto Rico, Mayagüez; José P. Rosado, Museum of Comparative Zoology; and Barbara Stein, Museum of Vertebrate Zoology, University of California, Berkeley. John E. Cadle generously provided field notes on his work in the region, and James R. Dixon provided copies of field notes of R. H. Dean. The black and white photographs were printed by John E. Simmons, and the illustrations of tadpoles were rendered by Arvid Aase; both have my sincere thanks. Also, I thank Richard O. Prum for introducing me to the sound analysis program, Canary™. Finally, an earlier version of this manuscript greatly benefited from thorough review by Stefan Gorzula and Marinus S. Hoogmoed; I am deeply grateful to them for additional information and for their helpful comments.

MATERIALS AND METHODS

This paper is based on the study of 986 frogs, 46 lots of tadpoles, and 7 lots of eggs; of these, 708 frogs, 39 lots of tadpoles, and the 7 lots of eggs were among the collections that were made between El Dorado and the Gran Sabana by Duellman and his associates on 15–26 July 1974 and 25–29 January 1979. The same region was visited by Hoogmoed on 14 May–10 June 1978. All localities on the road between El Dorado and Santa Elena de Uaiarén on the Brazilian border are designated by kilometer distances on that road; these were conveniently marked by posts, with Km 0 being the bridge over the Río Cuyuni (= Puente Cuyuni) at the south edge of El Dorado. All localities are in Estado de Bolívar, Venezuela. Elevations were deter-

mined from a hand-held aneroid altimeter; temperatures were recorded on a Taylor maximum-minimum thermometer, and rainfall was measured in a rain gauge. Because of the system's wide application in ecological studies in the neotropics, I designate vegetation types by Holdridge's (1947; 1967) bioclimatic scheme, as mapped by Ewel et al. (1976), but in the following section correlations are made with the vegetation areas mapped by Huber and Alarcón (1988).

Specimens collected by Duellman and his associates are deposited in the Natural History Museum, University of Kansas (KU), and those by Hoogmoed in the Nationaal Natuurhistorisch Museum in Leiden, formerly Rijksmuseum van Natuurlijke Historie (RMNH). Material

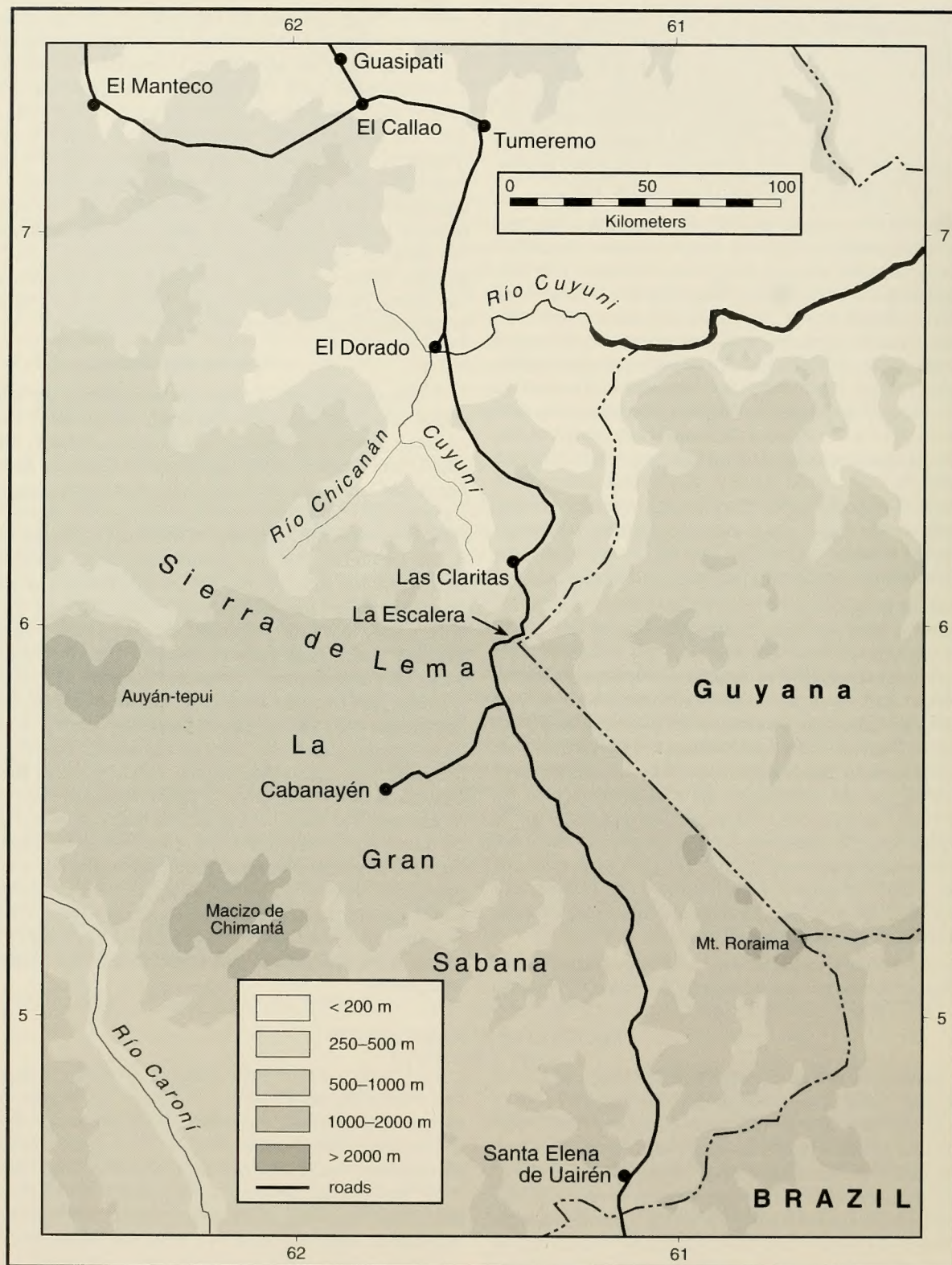


Fig. 1. Map of La Escalera Region showing localities mentioned in accounts of species and shown in profile (Fig. 2).

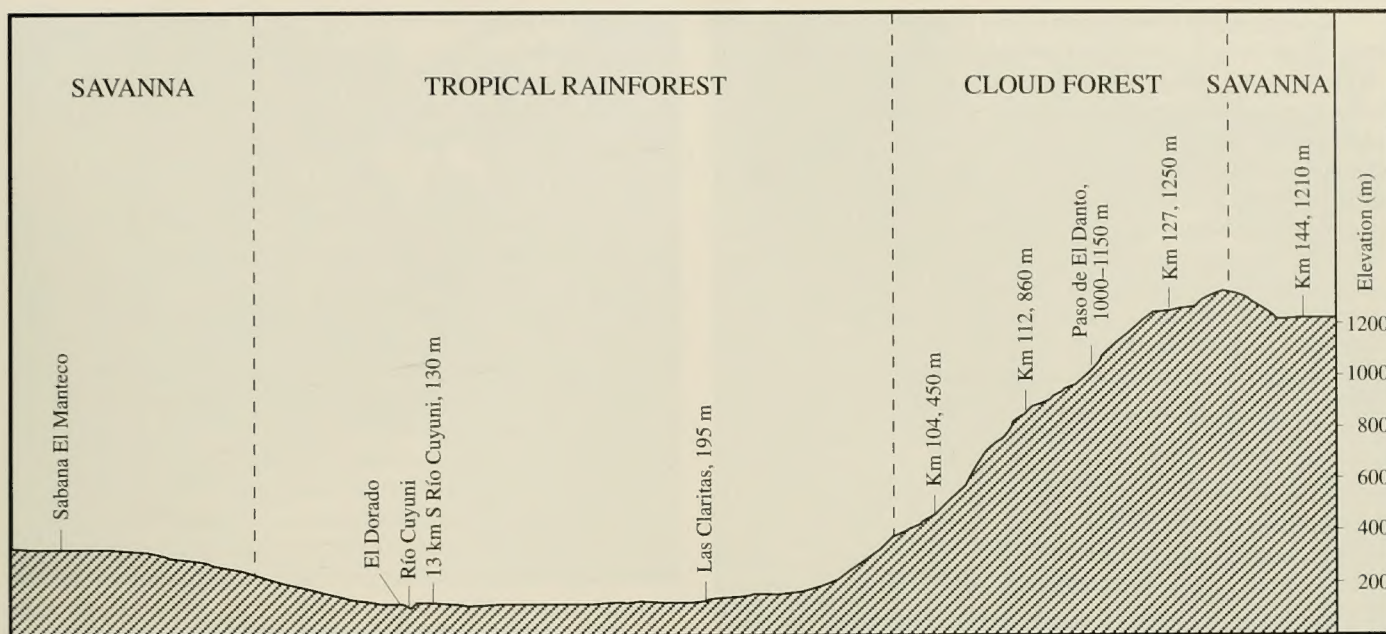


Fig. 2. Profile of La Escalera region, northern part of La Gran Sabana, and lowlands to the north. Region between Sabana El Manteco and Las Claritas foreshortened.

listed from other institutions includes the British Natural History Museum (BM); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Sociedad de Ciencias Naturales La Salle (SCNLS) in Caracas, Venezuela; Texas Cooperative Wildlife Collection, Texas A&M University (TCWC), and University of Puerto Rico, Mayagüez (UPRM).

All specimens in KU and RMNH were preserved in 10% formalin; all except larvae were subsequently transferred to 70% ethanol for storage. Recordings of calls were made on a Uher 4000 tape recorder with a Uher microphone. Recordings were analyzed using the software, Canary™ Version 1.2, on a Macintosh computer. The graphs

were generated using the software, Adobe Freehand™ Version 5.5, on a Macintosh computer. Measurements of morphological features and calls were taken in the manner described by Duellman (1970); measurements of frogs and tadpoles are in millimeters, and snout-vent length is abbreviated SVL. Webbing formulae were determined by the method proposed by Savage and Heyer (1967), as modified by Myers and Duellman (1982). Tadpoles were staged according to Gosner (1960), and larval terminology follows Altig and Johnston (1989). In the lists of materials in the accounts of species, the site at 13 km N and 1 km E of the bridge over the Puente Cuyuni is designated simply as Km 13, and C&S = cleared-and stained-skeletal preparation.

DESCRIPTION OF REGION

The terrain between El Dorado and the foot of the Sierra de Lema is slightly undulating at elevations between 125 and 235 m. There are many small streams and the large Río Cuyuni, which flows eastward to become an affluent of the Essequibo River in Guyana. The steep north slope of the Sierra de Lema rises about 1000 m in just a few kilometers (airline), but the sinuous road covers 50 km from the base to the crest. Throughout nearly all of this area the only disturbance is the road; no agricultural clearings are present. The Sierra de Lema has an elevation of 1270 m at the crest of the road; the range drops only about 50 m to the nearly flat Gran Sabana (Fig. 2).

According to the ecological map of Venezuela produced by Ewel et al. (1976), the lowland forest between El

Dorado and the foot of the Sierra de Lema is "humid tropical forest" in the Holdridge (1947; 1967) bioclimatic classification, and the north slope of the Sierra de Lema supports "very humid premontane forest" at lower elevations and "very humid lower montane forest" at higher elevations. The latter falls in the category of cloud forest, as evidenced by the presence of tree ferns and many terrestrial and arboreal bromeliads. Ewel et al. (1976) categorized the Gran Sabana as "humid premontane forest"; although climatically this categorization may be correct, the dominant vegetation of grasses and low bushes certainly does not constitute forest; the porous, white sandy soil characteristic of the savanna supports trees only in gallery forest along permanent streams.

A reasonable correlation exists between the ecological map (Ewel et al., 1976) and a vegetation map (Huber and Alarcón, 1988), in which the lowland forest is mapped as broadleaf subevergreen piedmont forest (*bosque ombrófilo plemontano sub-siempreverde*); trees in this forest form a canopy at heights up to 40 m, and the forest is characterized by three strata, a poorly developed shrub layer, and trees such as *Alexa confusa* (Leguminosae), *Amaioua ariculata* (Rubiaceae), *Anacardium giganteum* (Anacardiaceae), *Aspidosperma oblongum* (Apocyanaceae), *Drypetes variabilis* (Rosaceae), *Hymenaea coubaril* (Leguminosae), *Licania densiflora* and *L. discolor* (Rosaceae). The montane forests are mapped as broadleaf evergreen lower montane forest (*bosque ombrófilo basimontano siempreverde*) and broadleaf evergreen montane forest (*bosque ombrófilo montano siempreverde*); this dense forest is characterized by two strata with highest trees at about 25 m, well-developed undergrowth, and trees such as *Brysonima stipulacea* (Malpighiaceae), *Dimorphandra pennigera* (Caesalpiniaceae), *Licania micrantha* (Rosaceae) and *Podocarpus magnifolius* and *P. tepuiensis* (Podocarpaceae). The Gran Sabana is mapped as open savana grassland (*sabana graminosa abierta*); this vegetation is only about 1 m high and is composed of grasses (e.g., *Axonopus pruinosis*, *A. kaletukensis*, and *Trachypogon plumosus*), sedges (e.g., *Rhynchospora globosa* and *Scleria cyperina*), and in wet places, bromeliads of the genus *Brocchinia*. The dominant grassland on the Gran Sabana mostly results from fires; an estimated 70% of the fires on the Gran Sabana are set by Pemón people, who entered the region 200–300 years ago (Castro and Gorzula, 1986).¹

In 1974–1979, the forest along the road in the lowlands was slightly disturbed by intermittent logging and small clearings for agriculture; these were most numerous just to the north of Las Claritas. At the site 13 km S, 1 km E of El Dorado, the forest lacked a complete canopy. In the rainy season (July 1974), depressions were filled with water, but in the dry season (January 1979), the forest floor and leaf litter were dry. On the north slope of the Sierra de Lema, conditions become progressively wetter at higher elevations; rain fell at elevations above 650 m in January 1979. The humid conditions are evidenced by wet leaf litter and soils presumably throughout the year. The road was a mili-

tary road still under construction in July 1974; written permission was required at that time to travel on the road. Such was not the case in May–June 1978 and January 1979, by which time the road was being traversed by large trucks hauling logs from Brazil to Ciudad Bolívar.²

GAZETTEER OF PRINCIPAL COLLECTING SITES

The localities from which major collections were made are listed below with approximate coordinates derived from the International Travel Map of Venezuela, 1:1,750,000, International Travel Maps, Vancouver, Canada, 1994, supplemented by radar maps and coordinates provided by Stefan Gorzula. Most localities are given in kilometers on the El Dorado–Santa Elena de Uairén road; Km 0 is at the bridge over the Río Cuyuni (Puente Cuyuni). A few specimens were collected at other localities (e.g., Km 99, Km 116, Km 151) that are not in the following list. Of these, Km 99 is in lowland forest at the base of the Sierra de Lema; Km 151 is on the Gran Sabana, and the others are in the montane forest on the northern slope of the Sierra de Lema. Members of collecting expeditions who maintained field catalogues of specimens are noted by initials—MSH (Marinus S. Hoogmoed) and WED (William E. Duellman).

Cabanayén (Cabanayén).—05°36' N, 61°44' W, 1230 m. A Capuchino mission and small village on the Gran Sabana. Collections in the immediate vicinity of Cabanayén by MSH in May 1978 and WED in January 1979, and from gallery forest 5 km (by road) N Cabanayén by MSH in May 1978 and 12.9 km N of Cabanayén on the road to Salto El Toron by John E. Cadle in December 1980.

El Dorado.—06°41' N, 61°38' W, 130 m. A small town on the north bank of the Río Cuyuni. Collections from the town and from disturbed humid tropical forest at 1 km and 4 km N El Dorado in June 1978 by MSH.

Km 13.—06°37' N, 61°33' W, 130 m. A site 1 km E of El Dorado–Santa Elena de Uairén road in slightly disturbed humid tropical forest with about 90% forest cover, good leaf litter, and (in July) many temporary ponds (Fig. 3). Collections by WED in July 1974. On 26 July 1974, temperatures 22.0–28.0°C, and rainfall 45 mm in early evening. In January 1979, leaf litter dry and no temporary ponds.

Km. 38.—06°28' N, 61°27' W, ±150 m. Site in humid tropical forest. Collection by H. Heatwole in August 1962.

Km 104.—06°03' N, 61°20' W, 450 m. A site in disturbed, very humid premontane rainforest with many *Cecropia* and ferns on the lower northern slopes of the Sierra de Lema. Granitic and sandstone rocks, but soil primarily reddish brown clay; roadside ditches with flowing water; one rocky stream, and a few temporary pools (Fig. 4). On 25 July 1974,

¹ Stefan Gorzula (in litt., 29 March 1996) commented at length on fires and the vegetation on the Gran Sabana: "The vegetation on the Gran Sabana has been severely modified by fire.... The impact of burning has destroyed thousands of km² of Upland forest in this century alone!.... As you penetrate the Gran Sabana you will come across areas of burnt forest, secondary growth, burned secondary growth, bracken, and various types of grassland, each of which represent a stage in an on-going process of desertification. Interspersed through this are rocky areas with Upland scrub vegetation and peat bogs with herbaceous vegetation often containing species of flora that you would normally find on tepuys. We carbon dated the peat of one such bog, and the oldest (deepest) part was 4000 years old! I have flown more than 500 hours in helicopter over the Venezuelan Guayana, usually as a navigator. I have seen areas which are probably very similar to what the Gran Sabana would have been 500 years ago. That is to say, it was a mosaic of herbaceous vegetation over peat and Upland scrublands where there are rocky outcrops."

² Stefan Gorzula (in litt., 29 March 1996) noted that the road is now paved from El Dorado to Santa Elena de Uairén and that during the early 1980s, a gold rush turned Km 88 and Las Claritas into a shanty boom town with about 30,000 inhabitants. Gorzula flew over the area in 1986 or 1987 and noted that the forest had been cleared for about 0.5–1.0 km on either side of the road between El Dorado and Km 88, but that no major ecological damage was evident in La Escalera or on the Gran Sabana.



Fig. 3. Humid tropical forest along road 13 km S, 1 km E Río Cuyuni bridge. July 1974.



Fig. 4. Very humid premontane forest at Km 104 on El Dorado-Santa Elena de Uairén Road, 450 m. Bare area in middle is granite. July 1974.

temperatures 20.5–27.0°C, and rainfall 26 mm. Collections by WED in July 1974.

Km 112.—06°00' N, 61°23' W, 860 m. A site in very humid lower montane rainforest at midelevation on the north slope of the Sierra de Lema with a few palms, few bromeliads, and many ferns. Soil sandy. Two rocky streams, a small grassy roadside marsh, shallow rocky and muddy roadside ditches. On 20–21 July 1974, temperatures 17.0–26.0°C, and rainfall 61 mm. Collections by WED in July 1974 and January 1979.



Fig. 5. Very humid lower montane forest at Km 117 on El Dorado-Santa Elena de Uairén Road, 1000–1150 m. July 1974.

Km 117–119.—05°58' N, 61°22' W, 1000–1150 m. A site on the steepest ascent of La Escalera, known as Paso de El Danto, on the north slope of the Sierra de Lema. Very humid lower montane rainforest with many terrestrial and some arboreal bromeliads, many large-leafed vines (*Philodendron*), good mulch layer, and moderately thick growths of mosses on tree limbs, rocks, and banks of streams; soil sandy (Fig. 5). Many small, cascading streams and one river (Río El Danto) about 10 m wide with a series of three waterfalls (Salto de El Danto) (Fig. 6). On 18–19 July 1974, temperatures 18.0–25.0°C, and rainfall 10 mm. Collections by WED in July 1974 and by R. H. Dean in February 1981.

Km 127.—05°59' N, 61°24' W, 1250 m. A site just north of the crest of the Sierra de Lema in very humid lower montane with no canopy, many large-leafed vines (*Philodendron*) and arboreal bromeliads, and few ferns (Fig. 7). Terrain rather level with sandy soil, many small, shallow pools and streams with low gradients. On 23–24 July 1974, temperatures 15.0–26.0°C, and rainfall 32 mm. Collections by WED in July 1974 and January 1979.



Fig. 6. Salto de El Danto at Km 117 on El Dorado–Santa Elena de Uairén Road, 100–1150 m. July 1974.

Km 144.—05°53' N, 61°23' W, 1210 m. A site in the northern part of the Gran Sabana. Clumps of grasses less than 50 cm high predominated on white, sandy soil. Interspersed among grasses are sclerophyllous bushes 1–3 m high, and ant and termite nests (Fig. 8). A dense gallery forest exists along a meandering stream with steep banks. Ferns 1.0–1.5 m high are common between the grassland and the gallery forest. There are scattered sandstone and exfoliating granitic outcroppings, sluggish streams, and marshy ponds. On 22 July 1974, temperatures 13.0–24.0°C; no rain. Collections by WED in July 1974.



Fig. 7. Very humid lower montane forest at Km 127 on El Dorado–Santa Elena de Uairén Road, 1250 m. July 1974.



Fig. 8. Gran Sabana dominated by bunch grass at Km 144 on El Dorado–Santa Elena de Uairén Road, 1210 m. July 1974.

Las Claritas.—06°11' N, 61°26' W, 160 m. A town at Km 85 on the El Dorado–Santa Elena de Uairén road. Collections in disturbed humid tropical forest in immediate vicinity of village by MSH in May 1978.

ACCOUNTS OF SPECIES

ALLOPHRYNIDAE

Allophryne ruthveni Gaige, 1926

Material: Km 13, KU 166713–37, 166756–57 (C&S), 167818 (eggs).

On 26 July 1974, males were calling at night after a rain of 45 mm in the early evening; males called from leaves and branches of small trees and bushes, usually 1–2 m above the surface of the water in a flooded depression in the forest. One pair of frogs in axillary amplexus was on a branch of a bush 1.5 m above the water. This pair was placed in a plastic bag with water; during the night a clutch of approximately 300 pigmented eggs was deposited, but the eggs did not survive to hatching. Seventeen males have SVLs of 20.7–24.6 (\bar{x} = 22.6), and two females each have SVLs of 27.0. The vocal sac is greatly distensible; when inflated, it is much larger than the head.

In life, the dorsum was grayish tan to yellowish tan with brown to black markings; the posterior surfaces of thighs were dark brown to black with metallic cream flecks. The spots on the upper arm and heels were metallic cream, and the flanks were grayish brown with creamy yellow spots; the midventer was creamy tan, and the rest of belly was pinkish gray. The throat and ventral surfaces of the limbs were gray; the iris was dark reddish brown (Fig. 10). The call consists of a series of short notes. Four individuals were recorded, but the tapes subsequently were lost.

BUFONIDAE

Bufo granulosus Spix, 1824

Material: Cabanayén, RMNH 27107–16; Km 13, KU 166681–82; Km 144, KU 166683–96, Km 200, MVZ 175985; El Dorado, RMNH 27117; 1 km N El Dorado, RMNH 27118–19.

Only four males were found in the lowlands, where no breeding activity was observed. However, in the Gran Sabana, males were calling in a marsh at Cabanayén on 17 May 1978 and at a muddy pond at Km 144 on 17 July 1974; at the latter site, an adult female was found in a hole in the ground by day. Nine calling males from Km 144 have SVLs of 44.8–48.9 (\bar{x} = 46.7) and five gravid females have SVLs of 52.7–60.5 (\bar{x} = 57.6); seven males from Cabanayén have SVLs of 47.5–55.0 (\bar{x} = 50.6).

The advertisement call consists of a short trill. Analysis of one recording containing two calls (KU Tape 1327A, KU 166683, SVL 45.9) made at 16.5° C at Km 144 reveals the following parameters (Fig. 9): notes per call group 1, interval between notes 2.2 sec, duration of notes 0.95–1.77 (\bar{x} = 1.06) sec, pulse rate 27–32 (\bar{x} = 29.5) pulses per sec, dominant frequency 2.08–2.24 (\bar{x} = 2.16) kHz.

Bufo guttatus Schneider, 1799

Material: Km 112, KU 166711–12, 167631 (skeleton).

Three individuals were found in deep leaf litter on the forest floor at night; one male has a SVL of 120.3; two females have SVLs of 135.0 and 135.7. The skin on the dorsum is smooth; that on the flanks is smooth in the male, whereas the flanks of females have low, rounded tubercles.

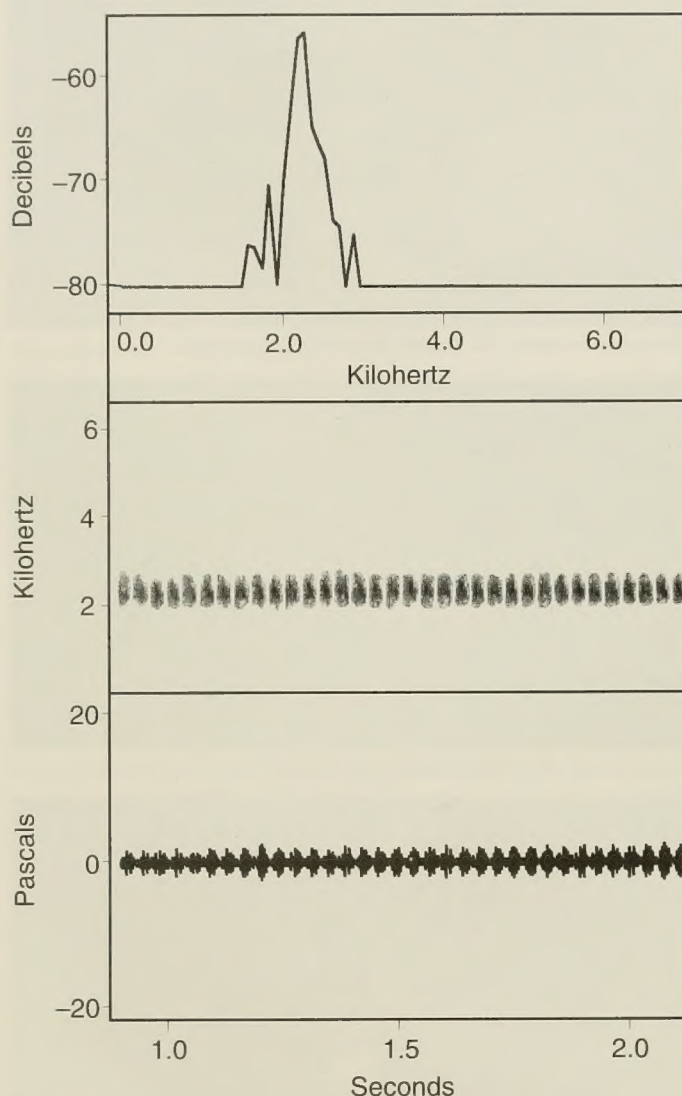


Fig. 9. Spectrum, spectrogram, and waveform of part of advertisement call of *Bufo granulosus*, KU Tape 1327A, Note 2. Recorded at 16.5°C; sampling frequency 22.3 kHz.

The venter is finely granular. Finger I is much longer than Finger II. Supraorbital, preorbital, and postorbital crests are not evident; parietal crests are low and convergent posteriorly. The supratympanic crest is thick and protrudes laterally. The canthal crest is poorly defined and protuberant laterally; it terminates posteriorly in a preorbital knob.

In life, the dorsum was reddish brown becoming yellowish tan dorsolaterally, but with reddish-brown tubercles; the side of the head, flanks, and outer surfaces of the limbs were brownish umber. The dorsolateral tubercles, spots on limbs, margin of lower jaw, and belly were yellow; the iris was dark reddish brown, giving a deep orange eyeshine at night. In preservative, the dorsum was reddish tan; the sides of the head, flanks, and limbs were



Allophryne ruthveni, KU 166717, female, 20.7 mm SVL.



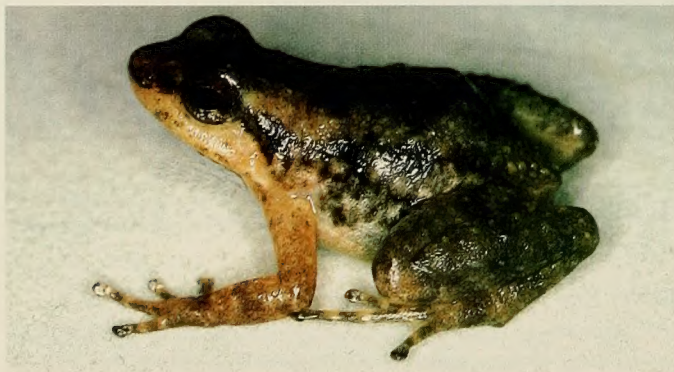
Bufo guttatus, KU 166711, female, 135.7 mm SVL.



Centrolene sp., KU 181128, male, 20.8 mm SVL.



Hyalinobatrachium orientale, KU 167371, male, 21.1 mm SVL.



Colostethus parkerae, KU 167329, female, 23.8 mm SVL.



Hyla crepitans, KU 166799, male, 47.0 mm SVL.



Hyla lemai, KU 166829, male, 28.9 mm SVL.



Hyla minuscula, KU 167134, female, 22.7 mm SVL.

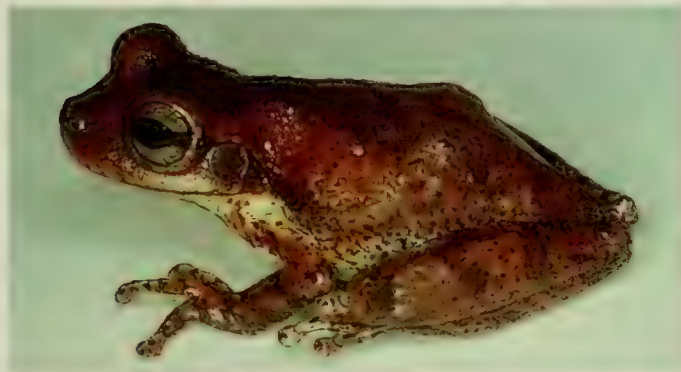
Fig. 10. Eight species of frogs from La Escalera region.



Hyla multifasciata, KU 166987, male, 51.7 mm SVL.



Hyla sibleszi, KU 167065, female, 35.0 mm SVL.



Tepuihyla rodriguezi, KU 167007, female, 35.9 mm SVL.



Eleutherodactylus pulvinatus, KU 166360, female, 32.7 mm SVL.



Leptodactylus rugosus, KU 166527, male, 59.2 mm SVL.



Leptodactylus sabanensis, KU 166562, female, 46.5 mm SVL.



Elachistocleis ovalis, KU 167389, male, 30.8 mm SVL.



Elachistocleis sp., KU 167409, male, 34.3 mm SVL.

Fig. 11. Eight species of frogs from La Escalera region.

dark brown, and the venter was brown with yellow spots (Fig. 10).

These large specimens compare favorably with three large females (RMNH 26966–68; SVL 128.9, 145.6, and 158.5) from Marowijne, Suriname. The coloration of the specimens from Suriname is like that in the individuals from Km 112, but in the specimens from Suriname, the skin on the dorsum of the body bears low, smooth warts. The difficulty in distinguishing between *Bufo guttatus* and *B. glaberrimus* Günther led Rivero (1961) to consider them to be conspecific. However, in addition to the characters mentioned by Rivero (1961), there seem to be differences in coloration. The venter is brown with distinct cream spots on the throat, chest and belly and narrow cream bars on the margin of the lower jaw in *B. guttatus*, whereas the venter is brown with diffuse cream spots on the posterior part of the belly and narrow cream bars on the margin of the jaw in *B. glaberrimus*. Moreover, *B. guttatus* is much larger than *B. glaberrimus* (SVL of adult male 72; Duellman, 1978).

Bufo marinus (Linnaeus, 1758)

Material: Cabanayén, KU 181069, RMNH 27120; Km 144, KU 166708.

Adults were found at night at the edge of a stream and in a marsh at Cabanayén and at the edge of a temporary pond in savanna at Km 144. Two adult males (KU 166708, 181069) with horny nuptial excrescences on Fingers I and II have SVLs of 110.6 and 95.3, respectively. This species was reported from Km 38 by Heatwole et al. (1965).

Bufo nasicus Werner, 1903

Hoogmoed (1977) reported a subadult (SCNLS 5949) from Km 126, a site in cloud forest near the crest of the north slope of the Sierra de Lema.

CENTROLENIDAE

Centrolene sp.

Material: Km 127, KU 181128.

An adult male with a SVL of 20.8 was on the upper side of a palm leaf about 2 m above a stream on the night of 27 January 1979. This specimen represents a species in the *Centrolene prosoblepon* group (sensu Ruíz-Carranza and Lynch, 1991) characterized by: (1) vomerine teeth absent; (2) bones green; (3) hepatic and pericardial peritonea white; visceral peritoneum clear (heart not visible); (4) dorsum in life uniform dark green (lavender in preservative); tips of fingers and toes yellow; iris pale silvery green with fine black reticulations; (5) webbing between outer fingers II 2–3 III 2+–2 IV; (6) webbing on foot I 1–2 II 1–2 III 1–3–IV 2–1+ V; (7) snout rounded in dorsal view, truncate in profile; (8) dorsal skin finely shagreen; (9) dermal folds absent on forearms and tarsi; (10) humeral spine present; (11) tympanum barely evident, oriented dorsolaterally with slight posterior inclination; (12) prepollex slightly enlarged; small, round, unpigmented, finely granular nuptial excrescence (Type I of Flores, 1985); prepollical spine not protruding externally; (13) pair of large, round tubercles posteroventral to vent; (14) Finger I slightly longer than Finger II. In life, the dorsum was uniform dark green; tips

of fingers and toes were yellow. The visceral peritoneum was clear, and the parietal peritoneum was white (heart not visible); the iris was pale silvery green with fine, black reticulations (Fig. 10).

The only named species of *Centrolene* in the Guayana region is *C. gorzulai* known only from the male holotype (SCNLS 11221) from an elevation of 1850 m on Cerro Auyantepuy (Ayarzagüena, 1992). This specimen differs from KU 181128 in five of the 14 characters listed above, but two of these are subjective; according to Ayarzagüena (1992), the webbing between outer fingers is II 2–2 III 2–2 IV, and the skin on the dorsum is smooth. Differences in three other features are more objective. According to Ayarzagüena (1992), all of the peritonea are transparent; a protruding prepollical spine is present, and the first and second fingers are equal in length. Because I have not had the opportunity to compare the holotype of *C. gorzulai* and confirm these apparent differences, I am reluctant to recognize the present specimen as a new species.

Hyalinobatrachium orientale (Rivero, 1968)

Material: Km 112, KU 181126, 181154 (eggs); Km 114, 181127; Km 117–119, KU 167371–73, 167847 (eggs), 167848 (tadpoles); Km 120, RMNH 26988.

On the nights of 18–19 July 1974 at Km 117–119, three males were calling from leaves of trees 2–3 m above a cascading stream. The call is a single “peep.” One male was adjacent to a clutch of pale green eggs on the underside of a leaf. Another clutch of eggs on the underside of a leaf hatched on 20 July 1974. Five hatchling tadpoles were virtually unpigmented; the gut was pale green, and the heart was visible. The largest tadpole has a body length of 3.4 and a total length of 14.0. At Km 112 on 25 January 1979, a male was calling from the underside of a leaf near two clutches of eggs, and Km 114 on 28 January 1979, a male was calling from the underside of a leaf over a stream. Five adult males have SVLs of 20.3–22.7 (\bar{x} = 21.4).

In life, the dorsum was pale lime-green with pale yellow spots and minute, black flecks; the forearms and shanks were greenish yellow with green transverse bars. The vocal sac was pale green, and the rest of venter, upper arms, thighs, hands, and feet lack pigment; the parietal peritoneum was clear (heart visible), and the visceral peritoneum and bones were white. The iris was deep bronze (Fig. 10).

These specimens were assigned to *Centrolenella orientalis* (= *Hyalinobatrachium orientale*) by Cannatella and Lamar (1986), who apparently were unconcerned about the hiatus of more than 500 km between the localities in the Sierra de Lema and the most proximate locality, Cerro Turumiquire; this gap includes the intervening dry forests, savannas, and Río Orinoco. Ayarzagüena (1992) reported specimens of this species from Km 130 and the Gran Sabana.

Hyalinobatrachium sp.

Ayarzagüena (1992) recognized “una *Centrolenella* del grupo *C. fleischmanni*” (= *Hyalinobatrachium* that is similar

to *H. orientalis*. Two specimens were reported from Salto El Danto (= Km 117–119).

DENDROBATIDAE

Colostethus parkerae Meinhardt and Parmelee, 1996

Material: Km 112, KU 167332–33, 167816 (tadpole), RMNH 19134, 19135 (tadpole), 19136–37; Km 117–119, KU 167328–31, 167835 (tadpoles).

At Km 112, two individuals were active by day in a muddy roadside ditch on 20 July 1974; at Km 117–119, four individuals were active by day on the rocky banks of the Río El Danto and a small rocky tributary on 18 July 1974. In addition to the type material (KU specimens; Meinhardt and Parmelee, 1996), three additional juveniles (RMNH 19134, 19136–37) are available; these have SVLs of 11.7, 13.3, and 18.0. In four living individuals (KU 167328–31), the dorsum was grayish tan with olive-brown markings. The throat was orange-yellow, and the rest of the venter was creamy yellow; the iris was pale bronze (Fig. 10).

Colostethus tadpoles were found in a shallow seep 5–10 cm deep on 19 July 1974 and in a small stream on 15 May 1978 at the type locality, and under a rock in small pool in a roadside ditch at Km 117–119 on 20 July 1974. Presumably these are tadpoles of *C. parkerae*, the only species of *Colostethus* known from the region.

Description of tadpole.—RMNH 19135, Stage 37 (Fig. 12). Type-IV tadpole (Orton, 1953. Total length 28.7; body length 10.1, 35.2% of total length, 1.4 × longer than wide, twice as long as high, 1.4 × wider than high; body in dorsal view bluntly ovoid, widest just posterior to level of eyes; body in lateral view highest posteriorly at rounded, slightly bulging gut; snout in dorsal view broad, bluntly rounded, in lateral view rounded above and inclined anteroventrally; eyes positioned and directed dorsolaterally; diameter of eye 1.2; interorbital distance 1.9; eye-naris distance 1.3; nares one-third distance from tip of snout to anterior margin of eye, moderately small, positioned and directed anterodorsally, lacking papillae on median margins. Spiracular tube sinistral, short, attached to body for its full length, inserting just below midline at about midlength of body; spiracular opening narrower than tube, directed posterodorsally; ventral tube moderately long, median at body, attached sinistrally for its entire length to ventral fin. Caudal musculature highest at tail-body junction, gradually narrowing to tip just proximal to end of tail; in lateral view, dorsal fin originating at tail-body junction, gradually increasing in height to about midlength of tail, maintaining that height nearly to rounded terminus; height of dorsal fin at midlength of tail 60% height of caudal musculature; comparable height of ventral fin 55% of musculature; ventral fin slightly deeper proximally than distally.

Oral disc ventral, not emarginate; two alternating rows of moderately long, pointed marginal papillae on lower labium; one row of small, blunt marginal papillae laterally on upper labium; broad median gap on upper labium and narrower gaps in lateral corners of disc; submarginal papillae absent; lower labium folding on itself laterally



Fig. 12. Tadpole of *Colostethus parkerae*, RMNH 19135, Stage 37. Total length 28.7 mm.

when oral disc closed. LTRF 2(1)/3; tooth rows about equal in length; teeth long; jaw sheaths moderately robust, rather coarsely serrate; each side of upper sheath sigmoid; lower sheath broadly V-shaped.

In preservative, dorsum and sides of body and dorsal edge of proximal one fourth of tail brown; rest of body and tail unpigmented, except for transverse area of melanophores on venter just anterior to intestines and scattered small groups of melanophores on caudal musculature, dorsal fin, and posterior third of ventral fin.

The other tadpoles are smaller and not so well preserved. Four individuals (KU 167835) in Stage 25 have body lengths of 10.5–11.2 (\bar{x} = 11.1) and total lengths of 28.2–29.0 (\bar{x} = 28.7). In life, the dorsum was grayish brown with dark brown flecks, and the belly was white; the tale was pale tan with blue flecks and brown reticulations, and the iris was coppery bronze. An individual (KU 167816; Stage 39) has a body length of 11.0 and a total length of 28.5. In life, the body was olive-tan with brown transverse marks, and the belly was gray; the tale was yellowish tan with brown flecks, and the iris was bronze.

Dendrobates leucomelas Steindachner, 1864

Material: Km 104, KU 167334.

An adult female with a SVL of 31.2 was under a log at the edge of a small stream by day on 25 July 1974. In life, the dorsum was golden yellow and black, and the venter was black with two small, bluish-white spots in the groin.

Epipedobates femoralis (Boulenger, 1884)

Material: Km 13, KU 167335.

One male with a SVL of 22.9 was on the forest floor by day. In life, the dorsum was brownish black; the dorsolateral stripes were bright yellow, and the spots at the bases of the thighs were bright orange.

HYLIDAE

Hyla boans (Linnaeus, 1758)

Material: Cabanayén, KU 181078; 185739; 12.9 km N Cabanayén, MVZ 176019; Km 13, KU 167824 (eggs); Km 112, KU 166770, 167836 (tadpoles), 167847 (young); Km 114, KU 181073, 181151 (tadpoles); Km 127, KU 181152–53 (tadpoles); Km 145, TCWC 60153.

Males were calling from more than 5 m above the ground from trees at Km 13 on 15 July, 1974, and one with a SVL of 97.4 was calling from a height of 4–5 m in a tree above the steep slope at Km 112 on 20 July 1974. A male with a SVL of 86.9 was calling from a tree on a steep slope on the night of 25 January 1979 at Km 114, and a juvenile with a SVL of 52.9 was on a bush in gallery forest on the night of 26 January 1979 at Cabanayén. A male with a SVL of 96.8 was in a tree in gallery forest at Km 145 on the night of 8 February 1981, and a male with a SVL of 109.0 was on exposed bedrock in a stream on the night of 28 December 1980 at 12.9 km N of Cabanayén. Males were calling from trees in February 1962 at Km 38 (Heatwole et al., 1965). The eggs from Km 13 were in a surface film in a mud basin at the edge of a forest pond; because no other frog in the region is known to construct a basinlike nest, the eggs are assigned to *Hyla boans*.

In life, KU 166770 had a brown dorsum with darker brown markings; the venter was cream, with a greenish-orange tint on the throat. The ventral surfaces of the discs were green, and the dorsal surfaces of the discs and webbing were dark brown. The iris was pale orange, and the palpebrum was finely reticulated with pale gold.

Tadpoles essentially matching the descriptions of tadpoles of this species from Darién, Panama (Duellman, 1970), and Santa Cecilia, Ecuador (Duellman, 1978), were found under leaves in a roadside ditch at Km 112 on 20 July 1974, in a leafy shallow ditch with a slight current at Km 114 on 26 January 1979, and in pools in a slow-moving stream at night at Km 127 on 27 January 1979. These tadpoles are in Stages 25–41 (Table 1). Two other tadpoles in Stage 25 from Km 127 are much larger (body lengths 14.5 and 18.0, and total lengths 44.0 and 54.5) than tadpoles in the same and more advanced stages; likewise another tadpole in Stage 33 from the same locality also is large—body length 18.4 and total length 55.2. Structurally, all of the tadpoles are alike, except for variation in the LTRF. Three of the normal-sized tadpoles in Stage 25 have a LTRF of 2(1)/3(1); the other two have a LTRF of 2(1)/4(1), and P4 is short and weakly keratinized. Thus, P4 apparently develops during Stage 25; the two large tadpoles in Stage 25 have well-developed P4s, as do all tadpoles in later stages of development. The median break in A1 is broad, whereas it is narrow and between a median anterior curvature in P1. One tadpole in Stage 30 and another in Stage 33 have a LTRF of 2(1)/5(1); P5 is short, fragmented, and composed of short, poorly keratinized teeth. A fifth posterior tooth row was not observed in tadpoles from Panama or Ecuador (Duellman, 1970, 1978).

In life, tadpoles from Km 112 were brown above with green flecks, and the venter was silvery white; the tail was

Table 1. Lengths (in mm) of tadpoles of *Hyla boans* at different developmental stages; means in parentheses.

| Stage | n | Body | Tail |
|-------|---|---------------------|---------------------|
| 25 | 5 | 8.3–11.9 (9.4) | 21.0–32.0 (24.6) |
| 28 | 4 | 14.7–15.0 (14.9) | 42.1–43.9 (43.1) |
| 30 | 2 | 15.0–16.8 (15.9) | 42.0–45.9 (44.0) |
| 34 | 1 | 15.0 | 40.6 |
| 35 | 1 | 16.5 | 47.5 |
| 36 | 3 | 15.5–16.5 (15.8) | 43.0–45.0 (44.0) |
| 41 | 2 | 15.0–16.5 (15.8) | 44.5–46.5 (45.5) |
| 46 | 1 | 17.0 | — |

tan with reddish-brown marks, and the iris was bronze. In those from Km 114, the body was pale tan with grayish-brown spots on the body and tail, and in those from Km 127, the body and tail were reddish brown. In preservative, all of the tadpoles have a pale tan dorsum; the venter is transparent, and the caudal musculature is pale tan with faint brown spots. White flecks are present on the body, caudal musculature and fins. In life, a recently metamorphosed young with a SVL of 17.0 had a brown dorsum with faint darker brown markings; the upper arms and heel stripes were cream, and the thighs were pale brown. The venter was gray, and the ventral surfaces of the feet were dark brown; the iris was pale bronze.

The call consists of a short, low-pitched growl. Analysis of one recording (KU Tape 1281, KU 166770, SVL 97.4) made at 20° C at Km 112 consists of 11 notes and reveals the following parameters (Fig. 13): notes per call group 1, note repetition rate 6 notes/min, duration of notes 0.12–0.15 (\bar{x} = 0.14) sec, pulse rate 120–140 (\bar{x} = 128) pulses/sec, dominant frequency 1190–1240 kHz. Two lower harmonics are present at about 400 and 800 kHz.

Hoogmoed (1990) resurrected *Hyla wavrini* Parker from the synonymy of *Hyla boans* and noted that the species differ in 26 characters. The characters of the specimens reported here agree with those of *H. boans*, except that they more closely resemble *H. wavrini* in having the discs on the toes essentially round (instead of transversely oval). All of the specimens have relatively small calcars, distinct vertical bars on the flanks, dark brown webbing, and gray throats.³

³ Stefan Gorzula (in litt., 16 March 1996) stated that he has collected *Hyla wavrini* at many localities in the Orinoco Delta and in Estado Amazonas and Estado Bolívar, Venezuela. He noted that males of *H. wavrini* attain SVLs of 119 mm and females 121 mm (exceeding sizes reported by Hoogmoed, 1990) and that the species does not construct basinlike nests. Gorzula observed that *H. boans* of the Gran Sabana are smaller than those in the lowlands and do not construct basinlike nests; instead, they breed in small, permanent streams. Available material is insufficient to ascertain definitive morphometric and structural differences, but the observations on tadpoles presented here confirm Gorzula's suspicion that the "*H. boans*" on the Gran Sabana may be specifically distinct from the widespread *H. boans* in the lowlands.

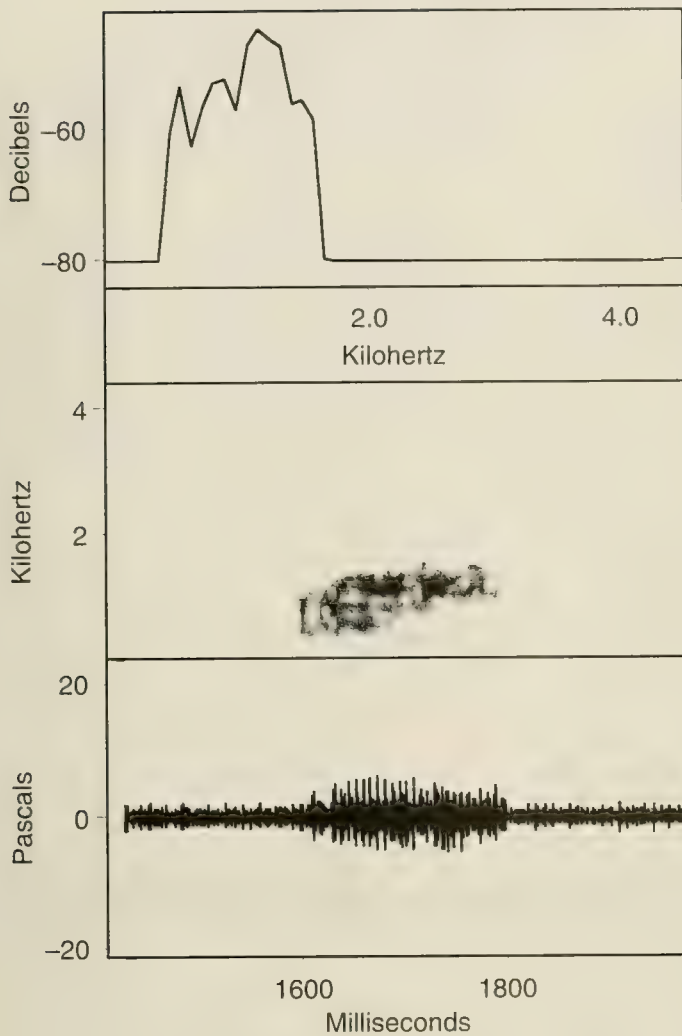


Fig. 13. Spectrum, spectrogram, and waveform of advertisement call of *Hyla boans*, KU Tape 1281, Note 6. Recorded at 20°C; sampling frequency 22.3 kHz.

Hyla crepitans Wied-Neuwied, 1824

Material: Cabanayén, KU 181074–75, 181076–77 (C&S), RMNH 27124–27; 5 km N Cabanayén, RMNH 27128–29; Km 13, KU 166784–98, 167826 (tadpoles) 167827 (eggs); Km 133, RMNH 27121; Km 144, KU 166799, 167825 (tadpoles); Km 146, RMNH 27122–23; 1 km N El Dorado, RMNH 27130–31.

At Km 13 on the nights of 15 and 26 July 1974, adults of both sexes were at the edges of roadside puddles and ponds and on vegetation adjacent to ponds in the forest; some males were calling. An amplexant pair was on the ground next to a pond. One clutch of eggs, presumably of this species, was in the form of a surface film in a roadside puddle. In the vicinity of Cabanayén on the Gran Sabana, males were calling from shallow marshes on 15–18 May 1978, and males and one amplexant pair were at the edge of a stream on the night of 26 January 1979.

Individuals of this species from the lowlands are predominately tan with reddish-brown markings, but frogs

from the Gran Sabana tend to be green, as evidenced from the following description of coloration of KU 166799 in life. Dorsum olive-green with dark olive-green markings; flanks greenish cream with dark olive-brown bars; throat greenish yellow; chest greenish white; belly orange-buff; ventral surfaces of limbs bluish green; webbing orange-tan; supraclavical and heel stripes creamy yellow; iris pale metallic green peripherally and pale gray centrally; tongue and lining of buccal cavity blue (Fig. 10). In preservative, specimens from the Gran Sabana have a darker brown dorsum than those from the lowlands; they also have more distinct bars on the thighs and a greater amount of dark pigment on the periphery of the chin. Furthermore, frogs from the Gran Sabana are slightly smaller than those from the lowlands. Twelve males from Km 13 and Km 12 from the Gran Sabana have SVLs of 53.4–62.3 (\bar{x} = 57.7) and 47.0–56.0 (\bar{x} = 51.3), respectively, whereas three females from Km 13 and two from Cabanayén have SVLs of 64.0–64.3 (\bar{x} = 64.1) and 57.7–62.0 (\bar{x} = 59.9), respectively.

Tadpoles were found in a muddy forest pool at Km 13 on 26 July. Six tadpoles in Stage 25 have body lengths of 10–17 (\bar{x} = 13.3) and total lengths of 38–47 (\bar{x} = 42.5). In life, the dorsum was brown with greenish lichenous marks, and the belly was greenish white; the tail was tan with brown marks, and the iris was creamy bronze. Two tadpoles (Stage 41) from a shallow muddy pond on 17 July at Km 144 have body lengths of 19 and 22, and total lengths of 54 and 60. The coloration differs slightly from tadpoles from the lowlands in that in life the body was olive-green above and yellowish white below; the caudal musculature was green with a bluish tint and brown reticulations, and the iris was bronze. Thus, the green coloration of the tadpoles parallels that of the adults on the Gran Sabana. These two lots of tadpoles agree with the description of tadpoles from Villavicencio, Colombia (Duellman, 1970), but both that description and the tadpoles differ from the description of tadpoles from Trinidad (Kenny, 1969); the latter have brown longitudinal stripes on the base of the tail.

Throughout its extensive range from Central America to eastern Brazil, *Hyla crepitans*, as now recognized, is variable in coloration, size, advertisement call, and calling sites. Consequently, it is highly likely that several species are recognizable within *H. crepitans*; one such probable recognizable taxon includes the frogs on the Gran Sabana.

Hyla geographica Spix, 1824

Material: Km 13, KU 166828.

At Km 13, an adult female with a SVL of 66.1 was on a bush adjacent to a pond in the forest on the night of 15 July 1974. In life, the dorsum was pale yellowish tan (at night); the flanks were bluish gray with white flecks. In preservative, there are many dark spots on the belly and a dark margin to the lower lip.

Hyla granosa Boulenger, 1882

Material: Las Claritas, RMNH 18708–09.

Two males were calling from leaves of bushes above a pond in secondary forest on the night of 9 June 1978.

Hyla lemai Rivero, 1971

Material: Km 112, KU 166829–36, 167760 (C&S); Km 125, RMNH 17839–40; 5 km N Cabanayén, RMNH 17838.

On the nights of 20–21 July 1974 at Km 112, males were calling from boulders in, and leaves, branches, and a log above a cascading stream. An amplexant pair deposited 54 unpigmented eggs (diameter 2.5) on a leaf in a plastic bag. At Km 125, a male was calling 30 cm above a stream and a female was on vegetation 1 m above a stream on the night of 10 June 1978, and on 18 May 1978, a male was in a tree 2 m above the water in gallery forest along a stream 5 km N Cabanayén. The sites of calling males and the deposition of unpigmented eggs on a leaf suggest that eggs normally are deposited on vegetation overhanging streams in which the tadpoles develop. Seven adult males have SVLs of 28.6–30.4 (\bar{x} = 29.6) and two females, 34.0–35.4 (\bar{x} = 34.7).

In life, the dorsum was yellowish tan with narrow, brown transverse marks on body and limbs and irregular golden marks on back (creamy-white spots in one individual). The ventral and hidden surfaces of hind limbs were lemon-yellow, and the fingers, toes, and webbing were orange. The throat was grayish white in males. The chest and median part of belly were white, and the belly pale was yellow laterally; the iris was pale silvery gray with minute, black flecks (Fig. 10). One subadult female (KU 181072) with a SVL of 29.3 was on a leaf of a bush on the night of 25 January 1979. This specimen has a different color pattern. At night, the dorsum was pale tan with brown markings and black flecks laterally; the venter was creamy yellow, and the iris was pale yellow with fine, black reticulations. By day, the dorsum was reddish brown with dark brown markings; the venter was creamy white, and the iris was greenish gray.

The call consists of a series of short whistles usually produced in groups of 3–5 notes with a slightly longer interval between than within groups. Analysis of three recordings (KU Tapes 1282–84; KU 166832–32; SVLs 30.3, 29.6, and 29.7, respectively) made at 21°C at Km 112 reveal the following parameters (Fig. 14): notes per call group 1–6 (\bar{x} = 3.5), note repetition rate about 120 notes/min, duration of notes 0.45–0.66 (\bar{x} = 0.55) sec, pulse rate about 300 pulses per second, dominant frequency 2.65–2.71 (\bar{x} = 2.68). The fundamental frequency is dominant; two other harmonics at 5.36–6.45 (\bar{x} = 5.40) and 8.00–8.07 (\bar{x} = 8.04) are evident.

Hyla microcephala Cope, 1886

Material: Km 13, KU 166878–81; El Dorado, RMNH 27132–43; 1 km N El Dorado, RMNH 27144–47; 4 km N El Dorado, RMNH 27148–54.

In the vicinity of El Dorado and at Km 13, males were calling from bushes and grasses in, and adjacent to, forest ponds on the nights of 15 July, 1974 and 8 June 1978, respectively. The species also was reported from Km 38 by Heatwole et al. (1965). Four males from Km 13 have SVLs of 22.3–23.4 (\bar{x} = 22.9).

The call consists of a series of short clicklike notes. Analysis of a recording (KU Tape 1285, 23°C, KU 166878,

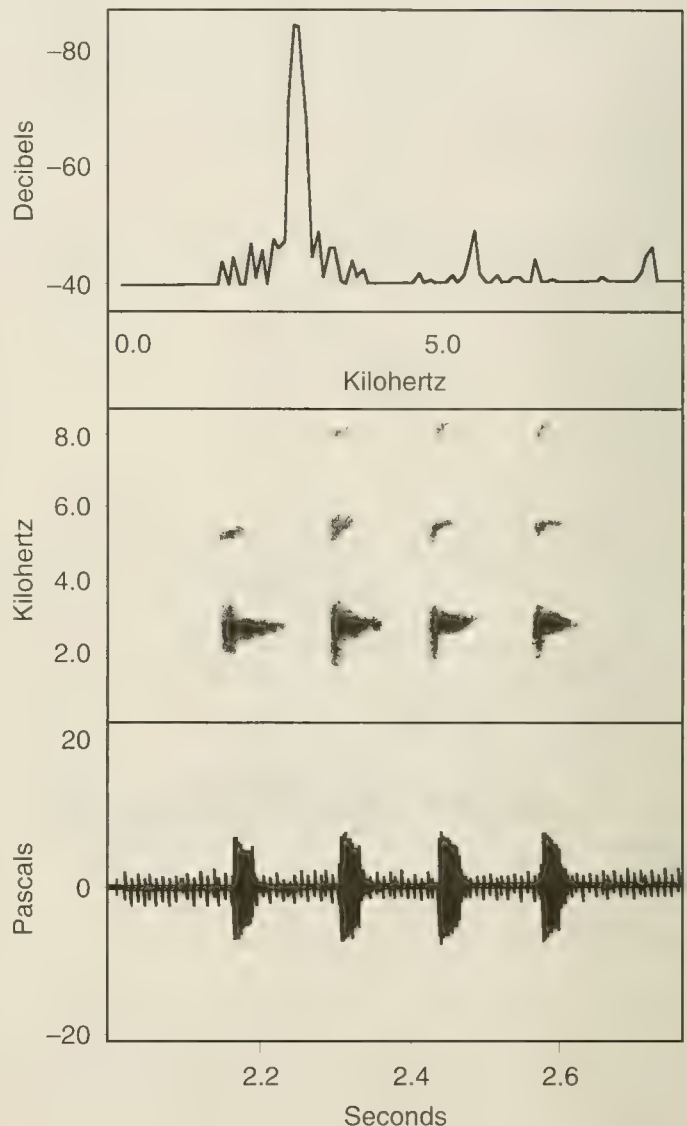


Fig. 14. Spectrum, spectrogram, and waveform of advertisement call of *Hyla lemai*, KU Tape 1284, Notes 1–4. Recorded at 21°C; sampling frequency 22.3 kHz.

SVL 23.1) at Km 13 containing seven call groups reveals the following parameters: intervals between call groups about 3.5 sec; notes per call group 2–12 (\bar{x} = 5.4), duration of notes 0.65–1.00 (\bar{x} = 0.88) sec, interval between notes 1.1–2.0 (\bar{x} = 1.5) sec, fundamental frequency 2.1–2.7 (\bar{x} = 2.3) kHz; dominant frequency 5.8–6.4 (\bar{x} = 6.2) kHz. Because of the weakness of the call, pulse rate could not be determined, and an illustration was not prepared.

Hyla minuscula Rivero, 1971

Material: Km 13, KU 167131–43; Km 82, RMNH 27155–60; El Dorado, RMNH 27161; 1 km N El Dorado, RMNH 27162–63.

Males were calling from leaves of bushes around a forest pond on the night of 15 July 1974 at Km 13 and from vegetation 40–60 cm above the water in a forest pond at Km 82 on the night of 14 May 1978. Nine calling males

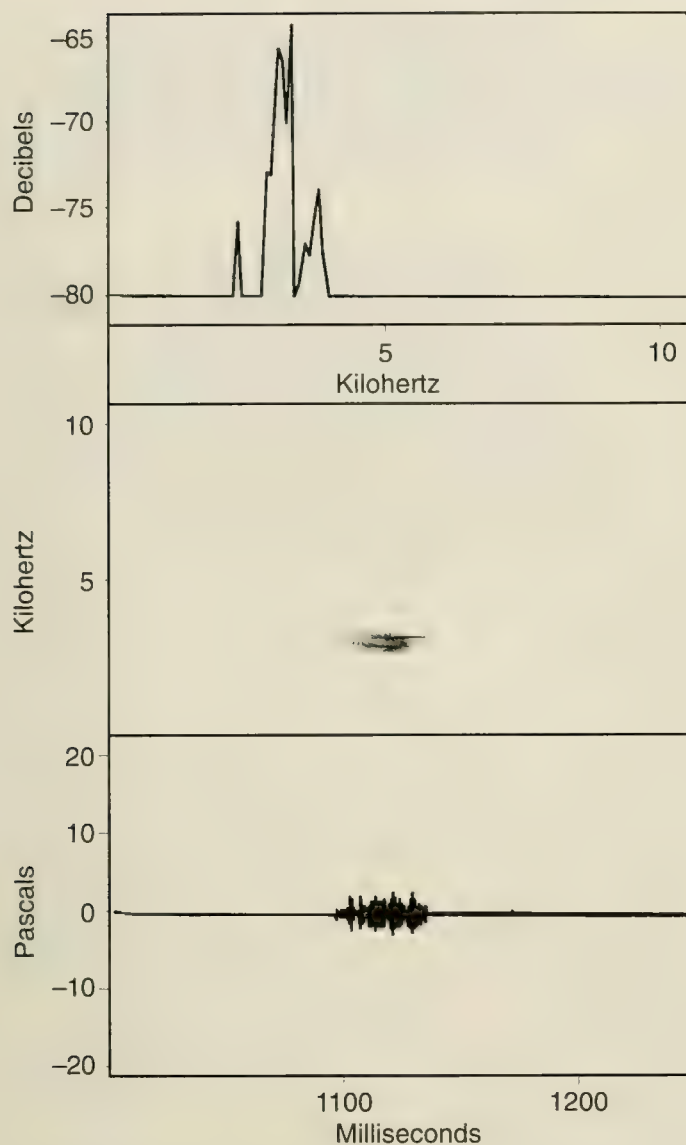


Fig. 15. Spectrum, spectrogram, and waveform of advertisement call of *Hyla minuta*, KU Tape 1312, Note 1. Recorded at 23°C; sampling frequency 22.3 kHz.

have SVLs of 18.9–20.6 (\bar{x} = 20.0) and four gravid females, 22.7–24.0 (\bar{x} = 23.3). At night, individuals from Km 13 had a pale yellow dorsum with cream dorsolateral stripes, and a pale green vocal sac. By day, the dorsum was yellow, and the flanks and sides of the head were grayish brown; the hands and feet were orange; the thighs were orange-yellow, and the belly was creamy white. The iris was red-bronze (Fig. 10).

The advertisement call consists of a series of soft chirps. Analysis of one recording (KU Tape 1312 of KU 167133, 18.9 SVL) made at 23°C at Km 13 reveals the following parameters (Fig. 15): notes per call group 1, interval between calls 1.6 sec, duration of note 0.28 sec, pulse rate 250 pulses/sec, dominant frequency 3.77 kHz, other harmonics at 2.11 and 4.58 kHz.

Hyla minuta Peters, 1872

Material: Cabanayén, RMNH 27209–11; Km 13, KU 166947–86; Km 104, KU 166914–17; Km 112, KU 166918–28, 167832 (tadpoles); Km 114, RMNH 27206–07; Km 117–119, KU 166929–30, TCWC 59780, 60145–46; Km 121, RMNH 27208; Km 127, KU 166895–913, 167828–29 (tadpoles), 181093–94, 181146 (tadpoles), RMNH 27197–205, TCWC 59781–82; Km 132, MVZ 175989–94, RMNH 27220–21; Km 133, RMNH 27165–96; Km 144, KU 166931–46, 167830–31 (tadpoles); El Dorado, RMNH 27212; 1 km N El Dorado, RMNH 27213; Las Claritas, RMNH 27214–19.

In the rainy season, this is the most abundant frog throughout the region. Although it is especially common in the lowlands, where the frogs congregate in large numbers at temporary ponds in the forest, it also is common around roadside ditches and puddles in the cloud forest on the steep slopes of La Escalera and at grassy ponds in the Gran Sabana. At Km 144, males were calling from grasses in a shallow marsh and from bare mud around a pond; one amplexant pair was on the mud bank, and another pair was on grass in the marsh on the night of 22 July 1974. However, in the dry season (January 1979), only three individuals were found—all in cloud forest at Km 127. The species also was reported from Km 38 by Heatwole et al. (1965).

Individuals from the lowlands are slightly larger than those from the Gran Sabana. Ten calling males and six gravid females from Km 13 have SVLs of 21.5–23.0 (\bar{x} = 22.4) and 24.1–25.9 (\bar{x} = 25.1), respectively; 10 calling males and 3 females from Km 144 have SVLs of 20.5–22.6 (\bar{x} = 22.1) and 23.8–24.5 (\bar{x} = 24.2), respectively.

Tadpoles were found in a muddy pond and in a shallow marsh at Km 144 on 17–18 July 1974, in a grassy pool at Km 112 on 21 July 1974, and in a pond at the edge of the forest at Km 127 on 23 July, 1974. At Km 112, tadpoles in Stage 25 (up to 30 in total length) were being eaten by *Pipa arrabali*. Presumed recently hatched tadpoles (KU 167831) have body lengths of about 6.0 and total lengths of about 13.0. Six tadpoles (KU 181146; Stage 25) have body lengths of 12.2–13.8 (\bar{x} = 13.0) and total lengths of 33.2–36.0 (\bar{x} = 34.9), and two from the same series in Stage 37 have body lengths of 14.0 and 14.2, and total lengths of 38.2 and 40.5. Two metamorphosing young (KU 167832) have SVLs of 13.5 and 13.8 and tail stubs of 17.0 and 11.7, respectively. In living tadpoles (KU 167828) from Km 127, the body and tail were yellowish tan with dark brown spots on the tail and gray-brown flecks on the body; the venter was white, and the iris was brassy, brown peripherally. In preservative, brown reticulations and spots are evident on the outer edges of the caudal fins; brown flecks or reticulations are present on the sides of the body of some individuals.

The tadpoles from La Escalera region have a deep caudal fin terminating in a long filament, and the dorsal fin originates at a point about 60% of the length of the body; the oral disc is bordered laterally and ventrally by a single row of small papillae, and the labial tooth row formula (LTRF) is 0/1. No distinct brown lateral line is present between the snout and the eye. The point of origin of the dorsal fin agrees with tadpoles from Trinidad (Kenny, 1969)

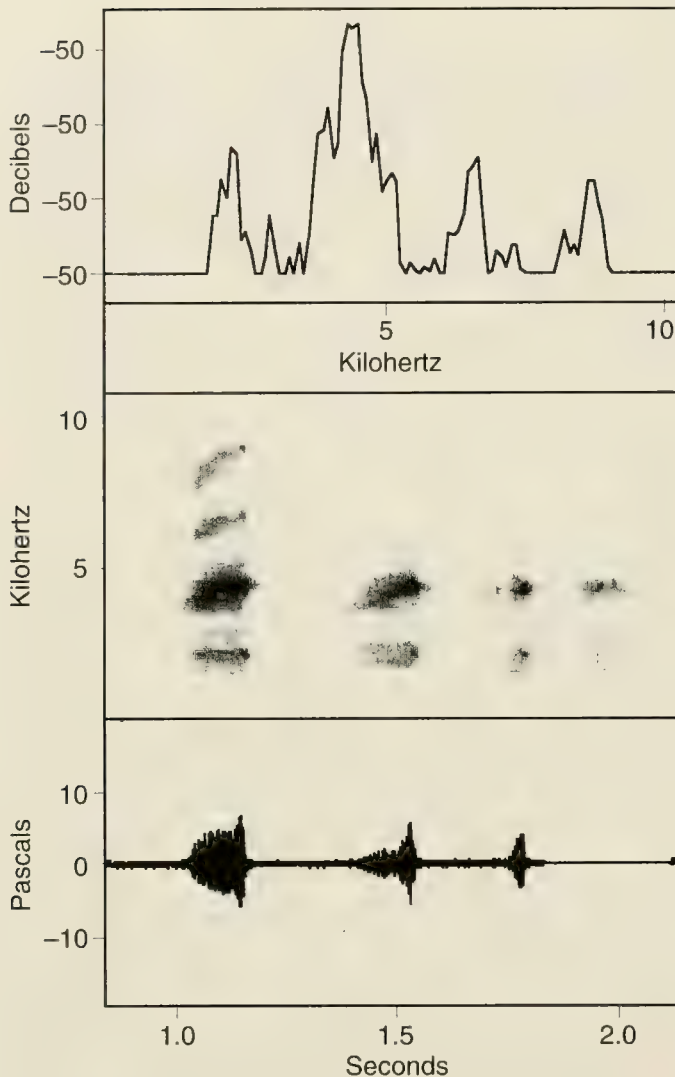


Fig. 16. Spectrum, spectrogram, and waveform of advertisement call of *Hyla minuta*, KU Tape 1289, Note 5. Recorded at 22°C; sampling frequency 22.3 kHz.

and Amazonian Ecuador (Duellman, 1978), but in tadpoles from Campo Grande, São Paulo, southeastern Brazil, the dorsal fin originates on the posterior edge of the body and is not as high as in the other tadpoles (Bokermann, 1963). The LTRF is 1/2 in Trinidad, 0/2 in Amazonian Ecuador, and 0/1 in southeastern Brazil. These differences in the larvae from widely separated sites in the broad range of the species suggest the possibility of *Hyla minuta*, as now recognized, being a composite of several species. The advertisement call consists of a short "wreeek" followed or not by 1–3 similar, shorter notes. Three recordings (KU Tapes 1286, 1288–89 of KU 166918, 166920–21, 22.6, 22.6, and 22.8 SVL, respectively) at 20°C at Km 112 contain 15 call groups and reveal the following parameters (Fig. 16): note repetition rate (primary notes only) 5–8 (\bar{x} = 1.3) notes/min, notes per call group 1–4 (\bar{x} = 1.3), duration of primary notes 0.11–0.18 (\bar{x} = 0.14) sec, duration of secondary

notes 0.05–0.16 (\bar{x} = 0.9, n = 5) sec, interval between notes in call group 0.17–0.24 (\bar{x} = 0.20) sec, pulse rate 170–200 (\bar{x} = 164), fundamental frequency 2.11–2.39 (\bar{x} = 2.24) kHz, dominant frequency 4.26–4.76 (\bar{x} = 4.50) kHz. Third harmonics are evident at 6.43–7.00 (\bar{x} = 6.68) kHz in all primary notes, and a fourth harmonic is present at 8.50–8.78 (\bar{x} = 8.64) kHz in three primary notes.

Hyla multifasciata Günther, 1859

Material: Cabanayén, KU 185741 185784 (tadpoles); 5 km N Cabanayén, RMNH 27222; Km 109, KU 181089; Km 112, KU 166987–89, 181090–92; 4 km E El Pauli, MVZ 176002.

One male was calling from 2 m up in a tree in gallery forest in savanna 5 km N Cabanayén on 18 May 1978. At Km 112, males were calling from ferns and low bushes along a roadcut at night, and noncalling males were found at the same site on 25 January 1979. Nine adult males have SVLs of 50.4–57.3 (\bar{x} = 52.9).

In living individuals (KU 166987–89), the dorsum was yellowish tan with brown transverse marks; the side of the head was olive-brown, and the posterior surfaces of the thighs and the webbing were chocolate-brown. The margin of jaw and tarsal, ulnar, supraclacal, and heel stripes were creamy white, and the throat was creamy orange with a gray suffusion marginally. The venter was cream, and the iris was pinkish copper (Fig. 11).

Two tadpoles obtained by Scott J. Maness from a pool in a stream at Cabanayén on 16 March 1975 presumably belong to this species. The tadpoles resemble those of the closely related *Hyla lanciformis* described by Duellman (1978), except that a poorly developed fourth posterior tooth row is present. Both tadpoles are in Stage 34 and have body lengths of 14.8 and 17.2 and total lengths of 38.2 and 44.5.

Description of tadpole.—KU 185784, Stage 34 (Fig. 17). Type-IV tadpole (Orton, 1953). Total length 38.2; body length 14.4, 38.7% of total length, 1.7 × longer than wide, twice as long as high, 1.2 × wider than high; body in dorsal view ovoid, widest at about midlength of body; in lateral view body highest at level of midgut; snout in dorsal view rounded, in lateral view inclined anteroventrally; eyes positioned dorsolaterally and directed more laterally than ventrally; diameter of eye 1.7; interorbital distance 2.4; eye-naris distance 1.6; nares slightly closer to eyes than to tip of snout, moderately small, positioned and directed dorsolaterally, having papillae on median margins; internarial distance 1.7. Spiracular tube sinistral, short, attached to body for its full length; spiracular opening slightly narrower than tube, directed posterodorsally at point below midline at about midlength of body; vent tube moderately short, broad, attached dextrally for its entire length to ventral fin; opening diagonal. Caudal musculature highest at tail-body junction, gradually narrowing to slender tip extending nearly to tip of tail; in lateral view, dorsal fin originating on caudal musculature at tail-body junction, gradually increasing in height to about midlength of tail and gradually diminishing in height posteriorly to acutely rounded tip; height of dorsal fin at midlength of

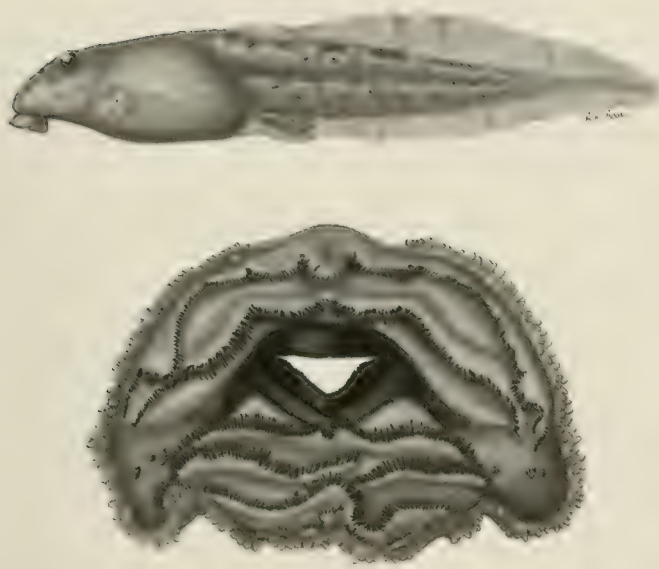


Fig. 17. Tadpole of *Hyla multifasciata*, KU 185784, Stage 34. Total length 44.5 mm.

tail about 70% height of caudal musculature; comparable height of ventral fin 50% of musculature; ventral fin lower than dorsal fin throughout length of tail.

Oral disc anteroventral, emarginate; single row of short, pointed marginal papillae with broad median gap on upper labium; submarginal papillae absent; lower labium folding on itself laterally when oral disc closed. LTRF 2(1)/4; A1 narrowly interrupted medially; tooth rows about equal in length, except P4, which is present as weak, fragmented row medially; teeth long, except in P4; jaw sheaths slender, finely serrate; upper sheath in form of broad arch; lower sheath broadly V-shaped (Fig. 17).

In preservative, flanks and dorsum of body grayish brown; posterior part of dorsum and caudal musculature tan with square middorsal brown blotches and small brown blotches laterally on tail; venter transparent.

The advertisement call consists of a low-pitched rattle produced sporadically. Analysis of a recording of one note (KU Tape 1292, KU 166987, SVL 51.7) made at 20°C at Km 112 reveals the following parameters (Fig. 18): duration of note 0.48 sec, pulse rate 35 pulses/sec, dominant frequency 1.77 kHz.

Hyla sibleszi Rivero, 1971

Material: 12.9 km N Cabanayén, MVZ 175995–601; Km 112, RMNH 18736 (tadpoles); Km 114, RMNH 18721; Km 117–119, KU 167058, 167834 (tadpoles), TCWC 60144, 69156; Km 120, RMNH 18722–27, 18733–35, 18737 (tadpoles); Km 127, KU 167059–67, 167768 (C&S), 181098–107, 181121 (C&S), 182085 (eggs), RMNH 18713–20; Km 129, RMNH 18710–12; Km 132, RMNH 18728–32.

At Km 127, males were calling from leaves of low herbs and bushes over water of a sluggish stream on the night of 16 July 1974, from ferns over slow-moving water in a roadside ditch on the night of 24 July 1974, and on leaves up to

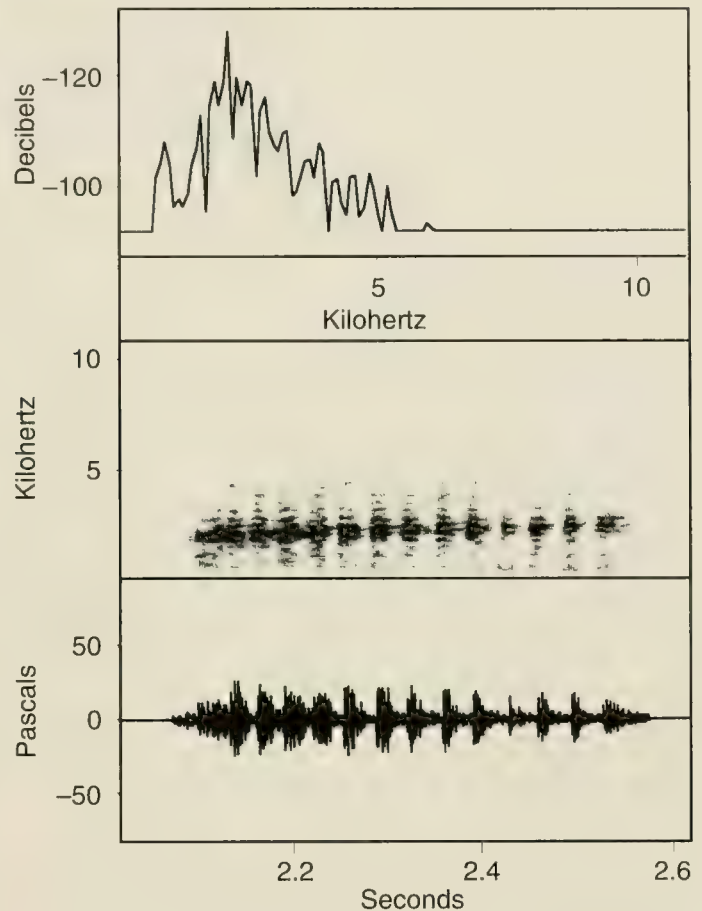


Fig. 18. Spectrum, spectrogram, and waveform of advertisement call of *Hyla multifasciata*, KU Tape 1292, Note 1. Recorded at 20°C; sampling frequency 22.3 kHz.

1.5 m above a stream on the night of 27 January 1979. One male was perched on a stem about 1 m above a stream on the night of 18 July at Km 117–119. At 12.9 km N Cabanayén on the night of 28 December 1980, males were calling from exposed bedrock in a stream in gallery forest. For those calling on 16 July 1974, the call was noted to consist of one or two soft, *Phyllomedusa*-like clucks, whereas for those calling on 27 January 1979 the call was noted to be a "wrack." A female (KU 181099) collected on 27 January 1979 was later in amplexus in a plastic bag and deposited a clutch of 42 pigmented eggs, each with a capsule of about 3.0 and ovum about 2.3 in diameter. Twenty-two males have SVLs of 29.8–34.9 (\bar{x} = 32.3) and three females, 34.2–35.7 (\bar{x} = 35.0).

In life, the dorsum was pale lime-green with or without tan or reddish-brown flecks and/or pale yellow dorsolateral and interorbital stripes; the latter were narrowly bordered by red in some individuals. The vocal sac was pale green; the transparent venter revealed a white peritoneum. The axilla and groin had a blue tint; the discs were yellow-orange, and the iris was pale yellowish bronze with black flecks (Fig. 11).

Two tadpoles in Stage 25 were obtained from small pools in a rocky, cascading stream at Km 117–119 on 19 July 1974; each has a body length of 10.5 and a total length of 30.0. In life, the body and tail were yellowish tan with a golden sheen on the tail; the iris was pale bronze. Hoogmoed (1979a), who thoroughly reviewed this species, provided a detailed description of tadpoles from Km 120.

Osteocephalus taurinus Steindachner, 1862

Material: Km 13, KU 167144–47.

On the night of 15 July 1974, one female was perched transversely on a small tree trunk in the forest, and a male and a juvenile were on the bank of a pond. When a female that was sitting on the edge of a road on the night of 26 July 1974 was picked up, it opened its mouth and emitted a loud buzzlike distress call. SVLs are: male 69.4, females 80.4 and 85.5, and juvenile male 49.6.

Rivero (1971a) referred a specimen (SCNLS 2763) from Km 88 and another individual (UPRM 2760) from the Alto Orinoco to *Osteocephalus leprieurii* (Duméril and Bibron). I have not examined the former, but the latter was examined and identified as *O. taurinus* by Trueb and Duellman (1971). Furthermore, the description of color pattern of the former specimen given by Rivero (1971a) more closely matches *O. taurinus* than *O. leprieurii*. Thus, it is most probable that SCNLS 2763 is *O. taurinus* and *O. leprieurii* is unknown from the region between El Dorado and Las Claritas.

Phrynohyas venulosa (Laurenti, 1768)

Material: Km 13, KU 167148–52.

Five males (SVL 77.5–85.3, \bar{x} = 81.0) were calling from branches of trees above a temporary pond in the forest on the night of 26 July 1974. In life, the dorsum was brown with darker brown markings; the venter was creamy yellow, and the iris was bronze with black reticulations.

Phyllomedusa bicolor Boddaert, 1772

Material: Km 13, KU 167133.

On the night of 26 July 1974 at Km 13, several males were calling from limbs of trees at heights of more than 2 m above the water in a forest pond. Heatwole et al. (1965) reported males calling from trees and an amplexant pair in a tree at Km 38 on 1 August 1965. In life, a male with a SVL of 91.1 had a uniform green dorsum; the venter was flesh-colored with an orange cast on the abdomen. The spots on the jaw, upper arm, toes, groin, hind limbs, and venter, and the stripes on the flanks and limbs, and in cloacal area were white bordered with dark brown; the iris was pale pinkish copper.

Phyllomedusa hypocondrialis (Daudin, 1802)

Material: Km 13, KU 167154–85, 167666 (skeleton), 167774 (C&S), 167841 (tadpoles); El Dorado, RMNH 27248; 1 km N El Dorado RMNH 27249–53; Las Claritas, RMNH 27254–56.

This small species seems to be the most abundant *Phyllomedusa* in the lowlands. Males were calling at Km 13 on 15 and 26 July 1974, at 1 km N El Dorado on 8 June

1978, and at Las Claritas on 9 June 1978. Males call from bushes in, and at the edge of, temporary ponds in the forest. Most individuals were within 1 m of the surfaces of the ponds.

Ten calling males from Km 13 have SVLs of 33.3–37.7 (\bar{x} = 35.2), and one gravid female, 44.0. In life at night, the dorsum in some individuals was green; in others, it was lavender-brown. By day, all individuals were pale green; the groin and hidden surfaces of the limbs were orange with black bars. The fingers and toes were pale brown; the labial, ulnar, tarsal, and supracloacal stripes were white, and the flanks were cream with black flecks. The venter was white, and the iris was silvery gray with black flecks.

Tadpoles presumably belonging to this species were so assigned because they are smaller than tadpoles of *Phyllomedusa bicolor* and *P. tarsius* in the same stages, and because they lack the yellow spot on the ventral fin characteristic of *P. tomopterna* (Duellman, 1978). These tadpoles also agree with the descriptions of *P. hypocondrialis* provided by Pyburn and Glidewell (1971) and Lescure et al. (1995). The tadpoles were in the deepest (\pm 0.5 m) central part of a muddy pond. In life, the body was silvery white with a golden and green sheen dorsally; the tail was unpigmented, and the iris was silvery white. Six tadpoles in Stage 25 have body lengths of 9.7–10.1 (\bar{x} = 9.9) and total lengths of 21.8–23.1 (\bar{x} = 22.4); six tadpoles in Stage 36 have body lengths of 13.1–16. (\bar{x} = 15.2) and total lengths of 35.8–40.7 (\bar{x} = 38.9).

The advertisement call consists of a harsh chirp repeated at intervals of 0.3–1.9 min. Analysis of a recording of one individual (KU Tape 1314, KU 167154, 35.0 SVL) made at 22°C at Km 13 contains three notes and reveals the following parameters (Fig. 19): notes per call group 1, note repetition rate 2.3 notes/min, duration of notes 0.28–0.30 (\bar{x} = 0.29) sec, pulse rate about 100 pulses/sec, dominant frequency 2.27–2.50 (\bar{x} = 2.40) kHz.

Phyllomedusa tarsius (Cope, 1868)

Material: Km 13, KU 167189–99, 167200 (skeleton); Las Claritas, RMNH 27257–58.

Males were calling on the nights of 15 and 26 July 1974 at Km 13 and of 9 June 1978 at Las Claritas. Most were observed on branches 1–3 m above the water in temporary ponds, but one was calling from a height of about 7 m. An amplexant pair was 1 m above the water on a *Heliconia* leaf. This species was reported (as *Phyllomedusa burmeisteri trinitatus*) from Km 38 by Heatwole et al. (1965). Eleven males have SVLs of 75.0–87.9 (\bar{x} = 82.8) and one gravid female, 94.3. In life, the dorsum was green; the flanks were creamy orange with pale blue flecks. The margin of lower jaw and the discs of fingers and inner two toes were cream; the other discs were brown. The throat and chest were gray, and the belly was pale salmon; the iris was coppery bronze with black reticulations.

This species has been reported previously from Venezuela as *Phyllomedusa trinitatis* Mertens. Kenny (1969) summarized information on coloration and reproductive

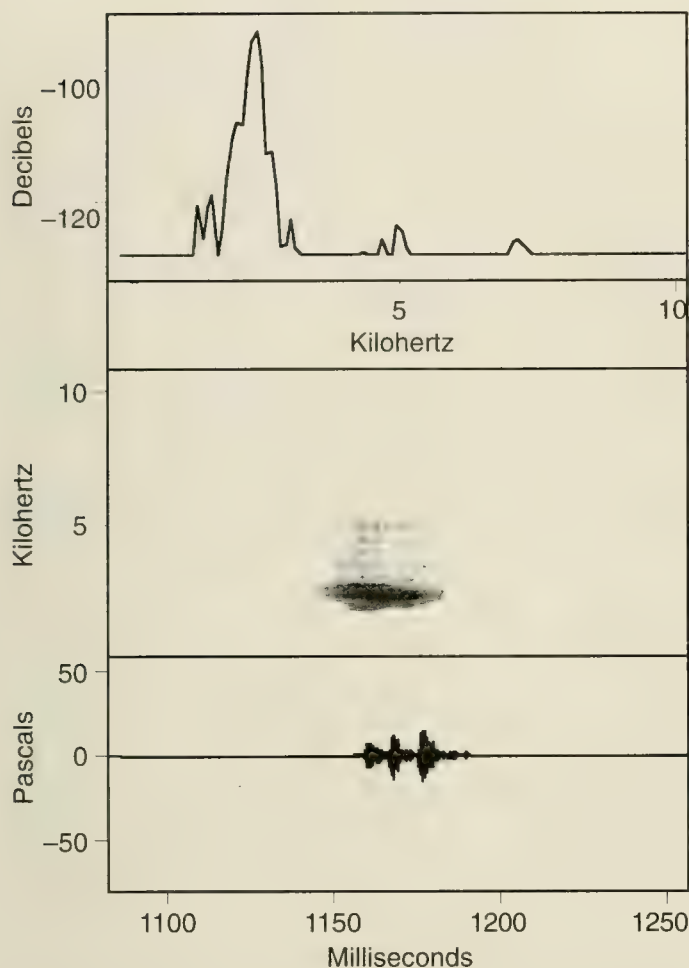


Fig. 19. Spectrum, spectrogram, and waveform of advertisement call of *Phyllomedusa hypocondrialis*, KU Tape 1314, Note 3. Recorded at 22°C; sampling frequency 22.3 kHz.

biology of that species on Trinidad. The specimens from Estado Bolívar agree with the summary of characters for *P. tarsi* in the Amazon Basin given by Duellman (1974). In fact, it is doubtful if the population on Trinidad (type locality of *P. trinitatis*) is specifically distinct from *P. tarsi*.

Phyllomedusa tomopterna (Cope, 1868)

Material: Km 13, KU 167188.

A single male with a SVL of 40.5 was calling from a *Heliconia* leaf near the edge of a temporary pond in the forest after a rain on the night of 26 July 1974. The flanks and limbs were orange with dark brown bars, and the iris was silver.

Scinax boesemani (Goin, 1966)

Material: Las Claritas, KU 192085–86, RMNH 27262–64, TCWC 60514–19.

Males were calling from vegetation 5–10 cm above the water in a temporary pond in secondary forest on the nights of 9 June 1978 and 7 February 1981. Eleven males have SVLs of 27.8–31.1 (\bar{x} = 29.2). In preservative, five in-

dividuals are uniform brown dorsally, whereas three have numerous pale tan spots on the back, and three others have small dark brown flecks on the dorsum; all specimens have distinct dark brown canthal and supratympanic stripes. Duellman (1986) provided a description and audiospectrogram of the advertisement call of this species recorded near Belém, Brazil.

Scinax danae (Duellman, 1986)

Material: Km 127, BM 1979.562–63 (paratypes), KU 167070 (holotype), 167071–83 (paratypes), 167088–91, 167769–70 (C&S), RMNH 21966–67 (paratypes).

On the night of 16 July 1974, males were calling (horizontally or head up) from leaves of herbs and bushes over a sluggish stream; on 23 July 1974, males were calling from herbs, small trees, bushes, and vines above and around a small, deep pond in forest, and on 24 July 1974, from low vegetation around a temporary pool at the edge of forest. Measurements, coloration in life, and description and audiospectrogram of the advertisement call were provided by Duellman (1986) in the description of the species. Duellman (1986:864) erroneously listed RMNH 21966–67 as “219660–67.”

Scinax exigua (Duellman, 1986)

Material: Cabanayén, RMNH 18637–50; Km 136, KU 167092 (paratype); Km 144, BM 1979.564–565 (paratypes), KU 167093 (paratype), 167094 (holotype), 167095–125 (paratypes), 167130 (paratype), 167838 (eggs), 167771–72 (C&S), 167849 (tadpoles), RMNH 21964–65.

At Km 144 on the night of 17 July 1974, males were calling from blades of grass in a shallow marsh and from grass along a sluggish stream; an amplexant pair that was about 1 m above the water on a bush subsequently deposited a clutch of pigmented eggs in a plastic bag. A gravid female was beneath a stone by day. Another individual was beneath a stone in grassland at Km 136. At Cabanayén on 17 May 1978, males were calling from forbs and grasses 10–20 cm above the water in a sluggish stream. Three solitary tadpoles from a shallow pool (\pm 15 cm deep) in a marsh at Km 144 possibly are assignable to this species. The largest tadpole is in Stage 25 and has a body length of 7.1 and a total length of 20.2. In life, the body and caudal musculature were dull brown, and there was little or no pigmentation on the caudal fins; the iris was grayish bronze.

Measurements, coloration in life, and description and audiospectrogram of the advertisement call were provided by Duellman (1986) in the description of the species. The numbers of three paratypes were given incorrectly by Duellman (1986:867); BMNH “1979.564–564” should read 1979.564–565, and KU “16792” should read 167092.

Scinax nebulosa (Spix, 1824)

Material: Km 82, RMNH 27265–71.

Males were calling from vegetation 40–60 cm above the water in a temporary pond on 14 May 1978. Six males have SVLs of 25.0–25.7 (\bar{x} = 25.7), and one female has a SVL of 34.5. In preservative, these specimens have bold black flecks in the groin and on the anterior surfaces of the thighs, vertical black bars separated by cream on the posterior surfaces of the thighs, and brown flecks on the throat.

Scinax rostrata (Peters, 1863)

Material: Km 13, KU 167037.

On 15 July 1974, one male having a SVL of 44.1 was calling from vegetation adjacent to a forest pond.

Scinax rubra (Laurenti, 1768)

Material: Km 13, KU 167041–57; El Dorado, RMNH 27272–77; 1 km N El Dorado, RMNH 27164; 4 km N El Dorado, RMNH 27283–64; Las Claritas, RMNH 27278.

On the nights of 15 and 26 July 1974, males were calling from the ground and low vegetation around temporary ponds in the forest; amplexant pairs were on low vegetation. On the night of 8 June 1978, males were calling from vegetation around temporary ponds in the vicinity of El Dorado. This species also is known from Km 38 (Heatwole et al., 1965). Males have yellow venters, whereas the venter in females is grayish white. Thirteen calling males and four gravid females from Km 13 have SVLs of 31.7–33.7 (\bar{x} = 32.4) and 33.8–38.6 (\bar{x} = 36.5), respectively.

Scinax x-signata (Spix, 1824)

Material: Km 13, KU 167068; El Dorado, RMNH 27279–82

At Km 13 on the night of 26 July 1974, a male having a SVL of 35.1 was calling from a *Heliconia* leaf about 1.5 m above the ground and 2 m from the edge of a forest pond. On 8 June 1978 at El Dorado, two males having SVLs of 35.5 and 38.5 were calling from vegetation above a temporary pond and an amplexant pair (SVL ♂, 38.3; ♀ 35.5) were on a tussock of grass in the pond. In life, KU 167068 had an olive-brown dorsum with dark brown markings; the hidden surfaces of the thighs were orange-yellow with brown bars. The belly was white, and the vocal sac was gray; the iris was bronze.

Sphaenorhynchus lacteus (Daudin, 1802)

Material: Km 13, KU 167220.

Only one (SVL 38.6) of several calling males was located and collected. They were calling from herbaceous plants just above the surface of the water in a pond in a forest clearing on the night of 26 July 1974. In life, the dorsum was uniform green; the belly and tarsal, ulnar, and supracloacal stripes were creamy white. The canthal stripes were dark brown, and the ventral surfaces of the limbs were bluish green; the iris was pale creamy bronze.

Stefania evansi (Boulenger, 1904)

Material: Km 112, KU 167239–56, 167672–74 (skeletons), 181112–16, RMNH 19450, 19454–58; Km 114, KU 181117; Km 116, KU 181118–20, 181122–25 (skeletons); Km 117–119, KU 167222–38, 167671 (skeleton), MCZ 64373 (holotype of *Stefania scalae*), TCWC 64124–26, UPRM 2204–05.

This species is closely associated with cascading mountain streams, where most individuals were found on clean boulders in, and at the edges of, streams, on branches over streams, and in the spray zone of waterfalls. Only one was observed on a mossy boulder; only one was on vegetation more than 50 cm above the water, and only one was perched on a fern. Those individuals on branches over streams usually were perched perpendicular to the branch.

On 20 July 1974 at Km 112, a female with 11 eggs on her back was perched on the branch of a small bush about 50 cm above the ground and several meters away from stream. No advertisement call was associated with this species.

Most of these specimens were included in Duellman and Hoogmoed's (1984) review of *Stefania*, in which *Stefania scalae* Rivero was placed in the synonymy of *Hyla evansi* Boulenger. Three specimens not included (TCWC 24124–25) are an adult female with a SVL of 65.0 and containing small ovarian eggs, and two subadult males with SVLs of 40.5 and 47.3; all three specimens lack pale dorsolateral stripes. Duellman and Hoogmoed (1984) summarized what then was known about the reproductive biology of this species; brooding females had been reported carrying 11, 12, 22, and 24 eggs. On 5 November 1982 at Km 123, Gorzula et al. (1983) found a female with 16 young on the dorsum. The young had SVLs of 18–20 (\bar{x} = 18.7) and were oriented with their heads peripheral to the middle of the back of the female.

Observations on the reproductive biology of captive individuals from Yurunai-tepui, Estado Bolívar, Venezuela (Mägdefrau and Mägdefrau, 1994) revealed that amplexus is axillary on land; as eggs are emitted by the female, the male grasps the eggs in his hind feet and pushes them anteriorly onto the back of the female. A photograph of the female with fresh eggs shows 11 eggs on her back (Mägdefrau, 1991). Egg-carrying females also were reported by Junger and Böhme (1991). Schlüter (1984) also provided illustrations of the call—a series of short clicks increasing in frequency and intensity over a period of 3 sec and having a dominant frequency of about 1 kHz.

Tepuihyla rodriguezi (Rivero, 1968)

Material: Km 117–119, MCZ 64740 (holotype), UPRM 2207, 2209–11; Km 144, KU 166998–7013, 167767 (C&S).

On the nights of 17 and 22 July 1974 at Km 114, males were calling from leaves of a bromeliad-like plant in a marsh and in shallow pools (2–6 cm) in grassland. Rivero (1968b) found individuals in bromeliads by day at Km 117–119. Measurements, coloration in life (Fig. 11), and description and audiospectrogram of the advertisement call of this species were provided by Duellman and Hoogmoed (1992), who allocated *Hyla rodriguezi* Rivero to *Osteocephalus*. The species was placed in the newly recognized *Tepuihyla* by Ayarzagüena et al. (1992b).

LEPTODACTYLIDAE

Adelophryne gutturosa

Hoogmoed and Lescure, 1984

A female (SCNLS 19925) with a SVL of 16 contained two eggs 2 mm in diameter; it was extracted from the stomach of a juvenile colubrid snake, *Chironius fuscus*, collected in April at Km 120 (Ayarzagüena and Diego-Aransay, 1985).

Adenomera hylaedactyla (Cope, 1868)

Material: Km 13, KU 166463–64; Km 104, KU 166338–39.

In the afternoon of 26 July 1974 at Km 13, two males with SVLs of 23.0 and 23.5 were calling from amidst grass. On 25 July 1974 at Km 104, a male with a SVL of 22.6 was calling at night from wet ground beneath grass and another male (SVL 23.6) was under a log by day; the call consisted of a series of notes lasting more than 4 min. In life, the calling male from Km 104 had a pale tan dorsum with dark brown spots, orange-tan lateral tubercles, and a yellow middorsal stripe; the venter was cream, and the iris was reddish brown.

Eleutherodactylus pulvinatus Rivero, 1969

Material: Km 117–119, KU 166359–60, MCZ 64741, TCWC 65554; Km 127, KU 166361–68, 181015–16.

This species was described on the basis of seven males from Paso El Danto (= Km 117–119); subsequent to the type description, no new information has been published on the species. In order to provide information comparable to that available for more recently described species of *Eleutherodactylus*, a diagnosis modeled after that of Lynch and Duellman (1997) is given here.

A member of the *Eleutherodactylus* (*Eleutherodactylus*) *martinicensis* series having (1) skin on dorsum smooth with scattered small tubercles (most numerous and largest in occipital, temporal and scapular regions, on upper eyelid, and on anterior flanks), that on venter areolate; discoidal fold prominent; dorsolateral absent; (2) tympanic membrane and tympanic annulus evident, its length one-third to one-half length of eye; (3) snout acutely rounded in dorsal view, rounded in profile; (4) upper eyelid bearing many small tubercles, much narrower than IOD; cranial crests absent; (5) vomerine odontophores triangular in outline; (6) males with vocal slits and unpigmented nuptial pads; (7) first finger shorter than second; discs on fingers broad; (8) fingers lacking lateral fringes; (9) ulnar tubercles present; (10) heel tubercles absent; outer tarsal tubercles absent; inner tarsal tubercle small; (11) inner metatarsal tubercle ovoid, 4–6 times size of conical outer metatarsal tubercle; supernumerary tubercles at bases of Toes III–IV; (12) toes lacking lateral fringes and webbing; fifth toe much longer than third, extending to middle of distal subarticular tubercle on Toe IV; (13) dorsum tan or pale brown with darker brown markings, usually consisting of an interorbital bar, labial bars, postorbital-supratympanic stripe, W-shaped mark in scapular region, chevron in sacral region, and transverse bars on limbs and digits; venter creamy tan; posterior surfaces of thighs uniform pale brown; (14) SVL in males 22.8–25.0, in females 30.7–32.7.

In living individuals at night (KU 166362–66), the dorsum was pale yellowish-tan with faintly darker markings; the venter was pale gray, and the vocal sac was dull yellow. By day, the dorsum was tan to olive-brown with dark brown markings and an orange-red W-shaped mark in the scapular region. The venter and posterior surfaces of thighs were gray; the iris was bronze with a median, horizontal red streak (Fig. 11). In preservative, all specimens, save one, have an interorbital bar, dark W-shaped mark in the scapular region, and a chevron in the sacral region. In life,

one juvenile (KU 181016) had a tan dorsum, dark brown flanks, and a diffuse dark brown middorsal stripe.

All individuals were collected at night; one was on a cliff, and the others were on leaves of herbs and bushes at heights of 1.0–1.5 m above the ground. Males were calling on the night of 23 July 1974 at Km 127; the call consists of a single peep emitted infrequently.

Leptodactylus bolivianus Boulenger, 1898

Material: Km 13, KU 166405–08, 167624 (skeleton), 167783 (tadpoles); Km 104, KU 167784–85 (tadpoles); Las Claritas, RMNH 27224.

Adults were on the ground next to forest ponds on the nights of 15 and 26 July 1974 at Km 13, and a male in breeding condition was found at Las Claritas on 14 May 1978. This species also is known from Km 38 and Km 52 (Heatwole et al., 1965). Three adult males have SVLs of 86.4–115.0 (\bar{x} = 99.5); two females have SVLs of 79.9 and 91.5, and a juvenile has a SVL of 49.4. In living specimens from Km 13, the dorsum was reddish brown with dark brown markings, and the venter was cream with gray mottling on the throat and chest; the labial stripe was pinkish tan, and the iris was bronze above and reddish copper below.

Tadpoles were in shallow, muddy ponds, where they took refuge under leaves on the bottom. In life, the dorsum of the body was dull olive-brown, and the venter was grayish white; the caudal musculature was olive-tan (orange-tan middorsally), and the iris was bronze. Seven individuals in Stage 25 have body lengths of 15.5–18.4 (\bar{x} = 16.9) and total lengths of 47.0–61.2 (\bar{x} = 51.2). Tadpoles of three species of *Leptodactylus* were found at Km 104; two of these, *L. longirostris* and *L. rugosus*, are distinctive morphologically, whereas the tadpoles assigned to *L. bolivianus* are larger and generalized *Leptodactylus* tadpoles, which match the description of that species provided by Heyer (1970).

Leptodactylus fuscus (Schneider, 1799)

Material: Km 13, KU 166414–34; 1 km N El Dorado, RMNH 27225.

At Km 13, all individuals were on the ground in the forest at night. Nine adult males have SVLs of 36.1–41.1 (\bar{x} = 39.4) and 12 gravid females, 37.3–45.6 (\bar{x} = 41.6).

Leptodactylus leptodactyloides (Andersson, 1941)

Material: Km 69, MVZ 176010–12.

On 18 December 1980, three individuals were under logs in partially disturbed lowland rainforest. Two adult males with two black prepollical spines on each thumb have SVLs of 36.3 and 37.9; one of these (MVZ 176011) has conspicuous orange ventrolateral glands. An adult female has a SVL of 46.4. In all three specimens, the posterior surfaces of the thighs have an orange-tan longitudinal stripe bordered below by dark brown. The throat and chest are grayish tan with diffuse cream spots; the spots are most distinct on the margin of the lower lip.

Leptodactylus longirostris Boulenger, 1882

Material: Cabanayén, RMNH 27226; 5 km N Cabanayén, RMNH 27227–28; 12.5 km S Cabanayén, MVZ 176005; Km 104, KU 166465, 167788



Fig. 20. Tadpole of *Leptodactylus longirostris*, KU 167789, Stage 39. Total length 36.0 mm.

(tadpoles); Km 112, KU 166463–77, 167789 (tadpoles), RMNH 27229–31; Km 117–119, KU 166474–79, 167625 (skeleton), TCWC 60139; Km 121, RMNH 27234, 27237–39; Km 126, MVZ 176014–15; Km 127, KU 166480–86, 167790 (tadpoles), 181027; Km 132, MVZ 176006; Km 136, KU 166487; Km 144, KU 166488–89; Km 151, KU 166490–91, 167791 (tadpoles).

This small species of *Leptodactylus* was abundant throughout the cloud forest and in the Gran Sabana. Some individuals were sitting at the edges of water in ditches or streams by day, but most were on the ground at night; many of the latter were partially sheltered by leaves or rocks, or they were sitting in the openings of holes in the ground. Other individuals, principally juveniles, were under rocks or logs by day.

Fifteen calling males and seven adult females have SVLs of 34.9–40.5 (\bar{x} = 37.8) and 40.3–50.0 (\bar{x} = 43.7), respectively. In life, the dorsum was gray, tan, or reddish brown with yellow to pinkish-cream dorsolateral stripes; the belly, ventral surfaces of limbs, and longitudinal stripe on posterior surfaces of thighs were bright yellow, and the throat was cream.

At various localities on 16–25 July 1974, tadpoles and metamorphosing young were found in ditches, where tadpoles buried themselves in the sediment or took shelter under leaves on the bottom. The partial description by Crombie and Heyer (1983) is augmented by the following more detailed description.

Description of tadpole.—KU 167789, Stage 39 (Fig. 20). Type-IV tadpole (Orton, 1953). Total length 35.5; body length 12.4, 34.9% of total length, 1.9 × longer than wide, 2.3 × longer than high, 1.2 × wider than high; body in dorsal view ovoid, narrowest anteriorly, widest at about two-thirds length of body; in lateral view body highest at level of midgut; snout in dorsal view bluntly rounded, in lateral view rounded; eyes positioned and directed dorsolaterally; diameter of eye 1.5; interorbital distance 1.7; eye-naris distance 1.5; nares about one-third distance from tip of snout to anterior margin of eye, moderately small,

Table 2. Lengths (in mm) of tadpoles of *Leptodactylus longirostris* at different developmental stages. Numbers in brackets in Total column are tail lengths; means in parentheses.

| Stage | n | Body | Tail |
|-------|----|---------------------|---------------------|
| 25 | 10 | 4.5–5.5 (5.0) | 14.7–16.2 (15.6) |
| 25 | 10 | 6.5–10.3 (8.4) | 17.0–28.8 (22.8) |
| 34 | 3 | 9.7–11.3 (10.3) | 28.0–32.2 (30.7) |
| 37 | 7 | 11.2–12.7 (11.9) | 32.0–36.0 (34.0) |
| 39 | 3 | 12.4–13.7 (12.8) | 35.5–36.0 (35.7) |
| 41 | 1 | 14.0 | 36.5 |
| 43 | 1 | 14.7 | [12.5] |
| 44 | 1 | 15.0 | [5.4] |
| 45 | 2 | 15.0–15.3 (15.2) | [1.6–2.0] (1.8) |
| 46 | 1 | 14.8 | — |

positioned and directed anterolaterally, lacking papillae on median margins; internarial distance 0.9. Spiracular tube sinistral, short, attached to body for its full length; spiracular opening about same diameter as tube, directed posterodorsally at point below midline at about midlength of body; vent tube short, broad, attached dextrally for its entire length to ventral fin. Caudal musculature highest at tail-body junction, gradually narrowing to slender tip extending nearly to tip of tail; in lateral view, dorsal fin originating on caudal musculature about 3 mm posterior to posterodorsal edge of body, slightly increasing in height to about midlength of tail and gradually diminishing in height posteriorly to pointed tip; height of dorsal fin at midlength of tail about 50% height of caudal musculature; comparable height of ventral fin 34% of musculature; ventral fin lower than dorsal fin throughout length of tail.

Oral disc anteroventral, emarginate; single row of long marginal papillae with broad median gap on upper labium; submarginal papillae absent; lower labium folding on itself laterally when oral disc closed. LTRF 2(1)/3(0/1); A1 broadly interrupted medially; P1 narrowly or not interrupted medially; tooth rows about equal in length, except P3 being shorter; teeth long, except in P3; jaw sheaths moderately slender, serrate; upper sheath in form of broad arch; lower sheath broadly V-shaped.

In life, body and tail pale brown mottled with dark brown; belly silvery white; iris bronze. In preservative, dorsum of body brown; snout, flanks, and venter transparent with white flecks; caudal musculature cream with small brown spots proximally; caudal fins translucent with white flecks.

The smallest tadpoles are in Stage 25; proportions remain about the same throughout development to Stage 41 (Table 2). The LTRF in tadpoles in Stage 25 is 2/2; P1 is narrowly interrupted medially in about half of all tadpoles examined.

Leptodactylus mystaceus (Spix, 1824)

Material: Km 69, MVZ 176007–08.

Two females with SVLs of 44.6 and 47.8 were under logs in partially disturbed lowland rainforest on 18 December 1980. Both have a distinct creamy-white labial stripe; the posterior surfaces of the thighs are brown with a creamy-white longitudinal stripe.

Leptodactylus pentadactylus (Laurenti, 1768)

Material: Km 13, KU 166495–97; Las Claritas, RMNH 27232.

On the night of 15 July 1974 at Km 13, a male was calling from the edge of a forest pond, a female was sitting in shallow water in a temporary pond, and a juvenile was on the forest floor. On the night of 9 June 1978 at Las Claritas, a male was on the forest floor. The species also is known from Km 38 (Heatwole et al., 1965). Two adult males have SVLs of 132.5 and 144.0 mm; one adult female has a SVL of 119.2 and one juvenile, 27.9.

Leptodactylus petersii (Steindachner)

Material: Las Claritas, RMNH 23701, TCWC 60155.

One of these specimens (RMNH 23701) was identified as *Leptodactylus petersii*, and the other (TCWC 60155) as *L. sabanensis* by Heyer (1994). The former is a male having a SVL of 35.0 and two black spines on each thumb. Examination of the latter specimen, a male having a SVL of 32.9 and a single black spine on each thumb, reveals that the venter is heavily mottled with brown except the postero-medial part of the belly, which is white; the posterior surfaces of the thighs are mottled dark brown and cream. These aspects of the color pattern agree more closely to the coloration of *L. petersii* than *L. sabanensis*. The species (as *L. podicipinus petersii*) was reported from Km 38 and Km 52 by Heatwole et al. (1965).

Leptodactylus rugosus Noble, 1923

Material: Cabanayén, KU 181028–30; 5 km N Cabanayén, RMNH 23909; 12.5 km S Cabanayén, MVZ 176016; Km 99, RMNH 23969; Km 103, RMNH 23906–08, 27233 (tadpoles); Km 104, KU 166498–524, 167627–28 (skeletons), 167795–96 (tadpoles), 167797 (young); Km 109, RMNH 23917–18 (tadpoles and young); Km 112, KU 166532–44, 167793–94 (tadpoles and young); Km 117–119, KU 166525–30, 167626 (skeleton), 167792 (tadpoles); Km 127, KU 166531; Km 199, MVZ 176013.

This moderately large, terrestrial *Leptodactylus* is abundant throughout the elevational gradient of the Sierra de Lema and also extends onto the Gran Sabana. Most individuals were associated with seepages and rivulets on granitic bedrock; this seems to be characteristic of the species throughout its range (Heyer, 1995). Adults and juveniles were on the ground at night and under rocks by day, and juveniles were also active by day. At Km 104 on 25 July 1974, males were calling at night from open ground, under bushes, and under rocks; a foam nest was under a boulder at the edge of a seep over granitic bedrock. On the night of 26 January 1979 at Cabanayén, three adults were at the edge of a small stream. Tadpoles and young were found in July 1974 and in May and June 1978. At Km 117–119 on 19 July 1974, tadpoles and metamorphosing young

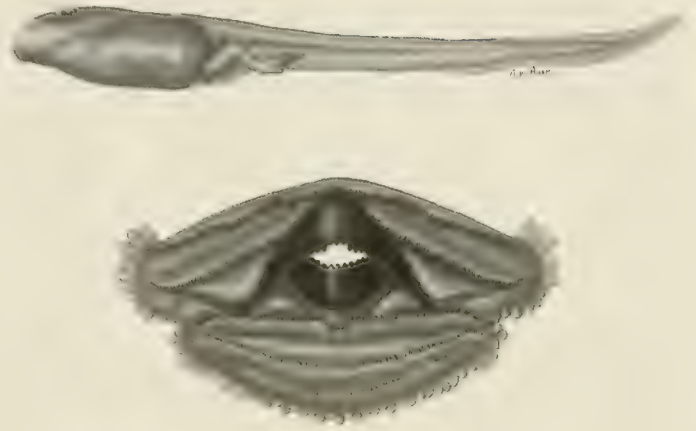


Fig. 21. Tadpole of *Leptodactylus rugosus*, KU 167792, Stage 39. Total length 40.0 mm.

were in a spring seepage flowing over granitic bedrock, where most individuals were in water less than 5 mm in depth; tadpoles with hind limbs moved with great agility over wet rock. Heatwole et al. (1965) reported 30 juveniles having SVLs of 12–30 and seven tadpoles from Km 109.

Eleven adult males and four females have SVLs of 55.2–64.0 (\bar{x} = 60.3) and 55.4–69.2 (\bar{x} = 59.9), respectively. A recently metamorphosed young has a SVL of 14.2, and three juveniles have SVLs of 21.8–35.9 (\bar{x} = 27.0). The inflated vocal sac is dark gray and protrudes laterally well beyond the angle of the jaw. In life, the dorsum was olive-brown to reddish brown with pale cream to grayish-tan markings. In juveniles and females, the throat, chest, and belly were white, and the ventral and posterior surfaces of thighs were orange; in males, the throat was gray; the chest and belly were dusky white, and the ventral surfaces of hind limbs were cream with brownish-gray mottling. The iris was pinkish bronze with a dark brown median, horizontal streak (Fig. 11).

Description of tadpole.—KU 167792, Stage 39 (Fig. 21). Type-IV tadpole (Orton, 1953). Total length 39.5; body length 11.8, 29.9% of total length, $1.7 \times$ longer than wide, $3.6 \times$ longer than high, $1.7 \times$ wider than high; body in dorsal view ovoid with slight constriction just posterior to eyes, narrowest anteriorly, widest at about three-fourths length of body; in lateral view, body highest posteriorly; snout in dorsal view rounded, in lateral view bluntly rounded; eyes positioned dorsolaterally and directed more dorsally than laterally; diameter of eye 1.6; interorbital distance 1.4; eye-naris distance 1.1; nares about midway between tip of snout and anterior margin of eye, moderately small, positioned and directed anterolaterally, lacking papillae on median margins; internarial distance 1.6. Spiracular tube sinistral, short, attached to body for its full length; spiracular opening about same diameter as tube, directed posterodorsally just below midline at about midlength of body; vent tube short, broad, attached dextrally for its entire length to ventral fin, with diagonal opening. Caudal musculature high-

Table 3. Lengths (in mm) of tadpoles of *Leptodactylus rugosus* at different developmental stages; means in parentheses.

| Stage | n | Body | Tail |
|-------|----|---------------------|---------------------|
| 25 | 10 | 4.5–5.3 (5.0) | 17.8–22.5 (20.4) |
| 25 | 4 | 7.2–7.5 (7.3) | 24.5–25.2 (24.9) |
| 28 | 3 | 7.5–8.3 (7.9) | 27.5–28.0 (27.7) |
| 30 | 3 | 8.4–8.7 (8.6) | 28.5–29.5 (29.2) |
| 31 | 1 | 8.5 | 26.7 |
| 32 | 1 | 9.0 | 34.2 |
| 33 | 1 | 9.2 | 35.3 |
| 34 | 1 | 9.6 | 37.7 |
| 37 | 2 | 10.2 | 39.8 |
| 38 | 2 | 10.6–11.7 (11.1) | 37.0–40.0 (38.5) |
| 39 | 1 | 11.8 | 39.5 |
| 41 | 9 | 10.4–12.5 (11.1) | 38.0–41.6 (40.1) |
| 42 | 2 | 11.6–11.8 (11.7) | 33.0–40.0 (33.5) |

est at tail-body junction, gradually narrowing to slender tip extending to tip of tail; in lateral view, dorsal fin, only a shallow ridge, originating on caudal musculature at point about three-fourths length of tail; ventral fin shallow, originating at about midlength of tail.

Oral disc ventral, emarginate; single row of short, blunt marginal papillae with broad median gap on upper labium; submarginal papillae absent; lower labium folding on itself laterally when oral disc closed. LTRF 2(1)/3(1); A1 and P1 broadly interrupted medially; tooth rows about equal in length; teeth longer in anterior rows than in posterior rows; jaw sheaths moderately robust, serrate; upper sheath in form of high arch; lower sheath broadly V-shaped.

Dorsum of body and caudal musculature and flanks brown; venter of body transparent with white flecks on throat; venter of caudal musculature cream; fins translucent with white flecks. In life, body reddish brown above with dark brown transverse marks; tail reddish brown with dark brown and greenish-blue spots; belly white; iris bronze with red median, horizontal streak.

Tadpoles in Stages 25–39 maintain a tail length of 70–75% of the total length (Table 3). Tadpoles in all of these stage have a LTRF 2/3. These tadpoles agree with the description of tadpoles from Km 109 (Heatwole et al., 1965).

The advertisement call consists of rapid trill increasing in pitch at the beginning of the note. Analysis of one recording containing six calls (KU Tape 1270 of KU 166502, 62.7 SVL) made at 22°C at Km 104 reveals the following parameters (Fig. 22): notes per call group 1, interval between calls 9–47 (\bar{x} = 21.4) sec, duration of notes 0.63–0.72 (\bar{x} = 0.68) sec, pulse rate 92.5–97.5 (\bar{x} = 94.4) pulses/sec, dominant frequency at beginning of note 1.67–2.15 (\bar{x} =

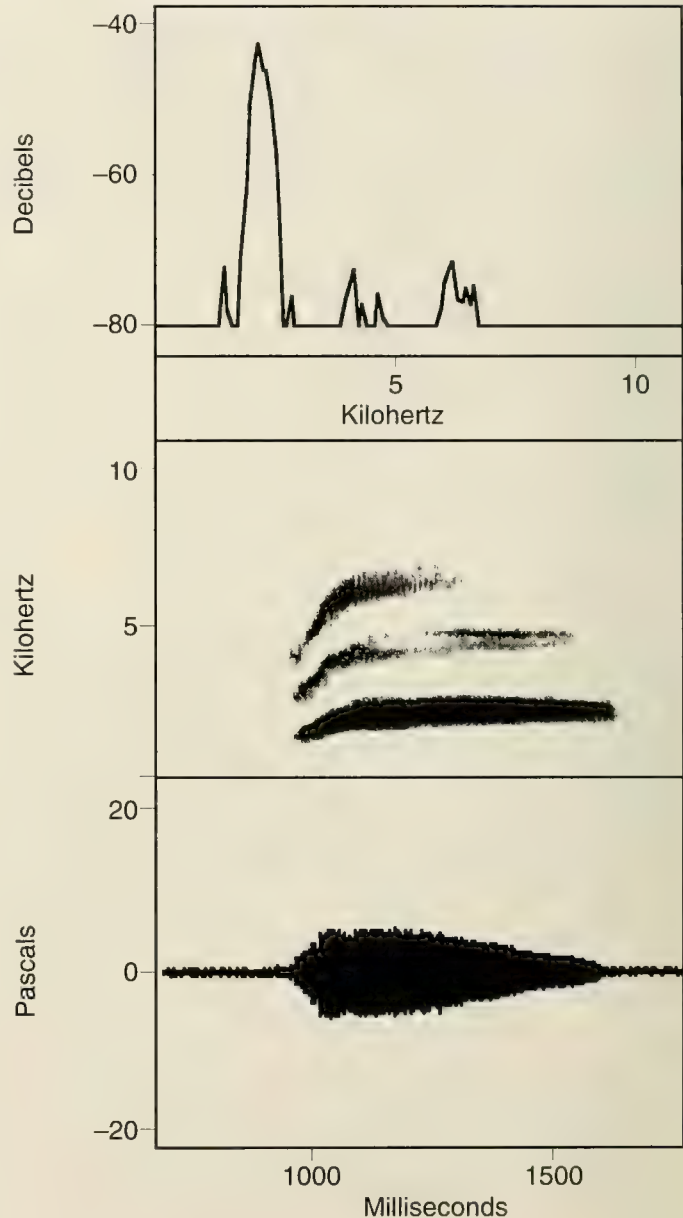


Fig. 22. Spectrum, spectrogram, and waveform of advertisement call of *Leptodactylus rugosus*, KU Tape 1270, Note 1. Recorded at 22°C; sampling frequency 22.3 kHz.

19.9) kHz, dominant frequency at middle of note 1.97–2.54 (\bar{x} = 2.31) kHz. The fundamental frequency is the dominant frequency; second harmonics at 4.15–5.00 (\bar{x} = 4.63) kHz in Notes 1–3 and 6, and third harmonics are evident at 6.30 and 7.30 kHz in Notes 1 and 3.

Leptodactylus sabanensis Heyer, 1994

Material: Cabanayén, RMNH 18407–08; Km 117–119, KU 167799 (tadpoles), 167800 (young); Km 120, RMNH 27235–36, 27240–44, 27247; Km 121, RMNH 23981; Km 126, RMNH 23979; Km 127, KU 166545–61, 167708 (tadpoles), 181031; Km 144, KU 166562–71; Km 145, TCWC 60148–49.

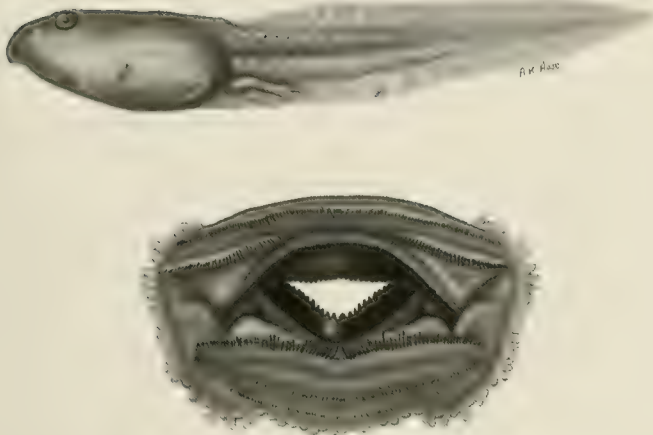


Fig. 23. Tadpole of *Leptodactylus sabanensis*, KU 167799, Stage 37. Total length 36.2 mm.

Throughout the duration of field work in July 1974 and May–June 1978, this species was found in cloud forest on the slopes of the Sierra de Lema and in the Gran Sabana. The frogs were under rocks and logs by day and on open ground at night, especially at the edges of small ponds and slow-moving streams. Fifteen adult males have SVLs of 39.2–44.6 (\bar{x} = 42.4) and eight females, 46.5–55.9 (\bar{x} = 52.0). All adult males have two sharp, black spines on each thumb; eight of 15 adult males have distinct yellowish-brown ventrolateral glands, whereas such glands are present in only three of eight adult females. In life, the dorsum was olive-brown to reddish tan with a darker interorbital triangle and transverse bars on the limbs, and the throat was gray; the venter was cream. There was a yellow spot in the groin and orange-yellow flecks on the posterior surfaces of the thighs; the iris was bronze with brown reticulations (Fig. 11).

At Km 117–119 on 19 July 1974, tadpoles were in, and recently metamorphosed young were adjacent to, a shallow, sand-bottomed stream with little gradient. At Km 127 on 20 July 1994, tadpoles were in a shallow pond.

Description of tadpole.—KU 167799, Stage 37 (Fig. 23). Type-IV tadpole (Orton, 1953). Total length 35.0; body length 12.0, 34.3% of body length, 1.5 × longer than wide, 1.9 × longer than high, 1.2 × wider than high; body in dorsal view ovoid, narrowest anteriorly, widest at about two-thirds length of body; in lateral view, body highest at level of midgut; snout in dorsal view and in profile bluntly rounded; eyes positioned and directed dorsolaterally; diameter of eye 1.4; interorbital distance 1.4; eye-naris distance 1.4; nares about one-third distance from tip of snout to anterior margin of eye, moderately small, positioned and directed anterolaterally, lacking papillae on median margins; internarial distance 1.5. Spiracular tube sinistral, short, attached to body for its full length; spiracular opening about same diameter as tube, directed posterodorsally at midline at about midlength of body; vent tube short, broad, attached dextrally for its entire length to ventral

Table 4. Lengths (in mm) of tadpoles of *Leptodactylus sabanensis* at different developmental stages. Numbers in brackets in Total column are tail lengths; means in parentheses.

| Stage | n | Body | Tail |
|-------|----|---------------------|-----------------------|
| 25 | 10 | 7.5–8.3 (8.1) | 19.2–21.8 (19.9) |
| 25 | 5 | 9.0–10.1 (9.5) | 23.7–25.1 (24.3) |
| 37 | 8 | 11.7–12.5 (12.2) | 32.8–35.0 (33.9) |
| 38 | 1 | 12.5 | 36.8 |
| 39 | 3 | 13.2–13.5 (13.3) | 39.5–40.0 (36.8) |
| 41 | 2 | 12.9–13.5 (13.2) | 39.0–40.0 (39.5) |
| 43 | 3 | 13.7–14.4 (14.0) | [13.1–17.0] (15.5) |

fin. Caudal musculature highest at tail-body junction, gradually narrowing to slender tip extending nearly to tip of tail; in lateral view, dorsal fin originating on caudal at tail-body junction, slightly increasing in height to about midlength of tail and gradually diminishing in height posteriorly to pointed tip; height of dorsal and ventral fins at midlength of tail about 70% height of caudal musculature.

Oral disc anteroventral, emarginate; single row of short marginal papillae with broad median gap on upper labium; submarginal papillae absent; lower labium folding on itself laterally when oral disc closed. LTRF 2(1)/3(0/1); A1 broadly interrupted medially; P1 narrowly or not interrupted medially; tooth rows about equal in length, except P3 being shorter; teeth moderately long, except in P3; jaw sheaths moderately robust, serrate; upper sheath in form of broad arch; lower sheath broadly V-shaped.

In life, body gray above and white below; tail brown with cream spots, and iris bronze. In preservative, body brown dorsally and transparent ventrally; caudal musculature tan; fins translucent; white flecks scattered on body and tail; faint brown reticulations on caudal musculature and fins.

Tadpoles in Stages 25–43 are available (Table 4). In the smaller tadpoles in Stage 25, P3 is poorly developed, whereas it is well developed in larger tadpoles in Stage 25 and in later stages. In life, three recently metamorphosed young having SVLs of 12.8–16.8 (\bar{x} = 14.2) were olive-brown above and white below.

This species was not encountered at elevations below 1000 m. Heyer (1994), who distinguished *Leptodactylus sabanensis* from *L. wagneri*, listed an individual (TCWC 60155) from Las Claritas at an elevation of 200 m; examination of this specimen reveals it to be *L. petersii*.

Physalaemus enesefae Heatwole, Solano, and Heatwole, 1965

Material: Km 13, KU 166574–82, 167801 (tadpoles); 1 km N El Dorado, RMNH 27259; Las Claritas, RMNH 27260.

On the nights of 15 and 26 July 1974, males were calling from secluded sites (e.g., under leaves) in shallow

temporary pools in the forest at Km 13. On the nights of 8 and 9 June 1978, males were calling at 1 km N of El Dorado and at Las Claritas, respectively. This species was described on the basis of three specimens from Km 38 and one from Km 52 (Heatwole et al., 1965). Eight males have SVLs of 25.9–27.7 (\bar{x} = 27.0), which are slightly smaller than the SVLs of 29 reported for three males by Heatwole et al. (1965), who noted that the SVL of the female holotype was 32. In life, the dorsum was reddish brown becoming grayish brown laterally, and the flanks were dark brown; the groin and hidden surfaces of the hind limbs were pale red. The venter was cream with grayish-brown spots, and the vocal sac was dark gray; the iris was pale creamy bronze.

Tadpoles were in a shallow pond in the forest on 26 July 1974. These tadpoles differ from the those of *Physalaemus pustulosus*. Those with hind limbs have pink on the thighs; because this color corresponds with the rose-red thighs of adult *P. eneseae*, the tadpoles are assigned to that species.

Description of tadpole.—KU 167801, Stage 39. Type-IV tadpole (Orton, 1953). Total length 19.5; body length 8.0, 41.0% of body length, 1.5 × longer than wide, 1.8 × longer than high, 1.1 × wider than high; body in dorsal view ovoid, widest just posterior to eyes; in lateral view, body highest at level of midgut; snout in dorsal view bluntly rounded, in profile rounded above and inclined anteroventrally; eyes positioned dorsolaterally, directed more dorsally than laterally; diameter of eye 1.0; interorbital distance 1.3; eye-naris distance 1.0; nares about one-third distance from tip of snout to anterior margin of eye, moderately small, positioned and directed anterolaterally, lacking papillae on median margins; internarial distance 1.0. Spiracular tube sinistral, short, attached to body for its full length; spiracular opening about same diameter as tube, directed posterodorsally below midline slightly anterior to midlength of body; vent tube short, attached sinistrally for its entire length to ventral fin. Caudal musculature highest at tail-body junction, gradually narrowing to slender tip extending nearly to tip of tail; in lateral view, dorsal fin originating on caudal musculature at tail-body junction, increasing in height to about midlength of tail and gradually diminishing in height posteriorly to pointed tip; height of dorsal fin at midlength of tail about equal to height of caudal musculature; comparable height of ventral fin about 65% height of caudal musculature.

Oral disc anteroventral, emarginate; single row of short marginal papillae with broad median gap on upper labium; submarginal papillae absent; lower labium folding on itself laterally when oral disc closed. LTRF 2(1)/3; jaw sheaths moderately slender, serrate; upper sheath in form of broad, flattened arch; lower sheath broadly V-shaped.

In life, the dorsum was grayish tan, and the was belly white; the tail was tan, and the fins were clear except for brown marginal blotches. The thighs were pink; the iris was pale bronze. In preservative, apparently because of storage in formalin with a low pH, the tadpoles are transparent.

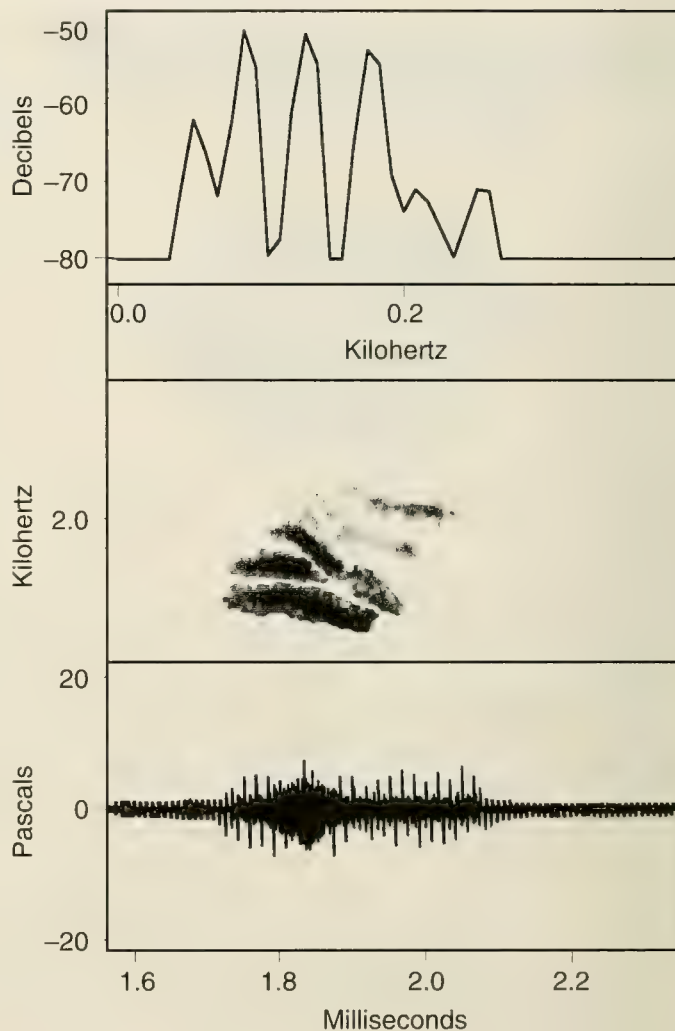


Fig. 24. Spectrum, spectrogram, and waveform of advertisement call of *Physalaemus eneseae*, KU Tape 1272, Note 6. Recorded at 23°C; sampling frequency 22.3 kHz.

Of eight tadpoles, one in Stage 31 has a body length of 7.2 and a total length of 16.5, and two in Stage 36 have body lengths of 8.0 and 8.2 with total lengths of 20.2 and 18.5, respectively; five tadpoles in Stage 39 have body lengths of 7.8–8.0 (\bar{x} = 7.9) and total lengths of 19.0–20.1 (\bar{x} = 19.7).

The call consists a short, frequency-modulated whine descending in pitch; no “chuck” calls, as emitted by *Physalaemus pustulosus* (Ryan, 1983), were produced. Analysis of one recording (KU Tape 1272, KU 166574, SVL 27.2) made at 23°C at Km 13 containing six notes revealed the following parameters (Fig. 24): notes per call group 1, note repetition rate 6 notes/min, duration of notes 0.12–0.14 (\bar{x} = 0.13), pulse rate 4.10–4.35 (\bar{x} = 4.24) kHz. Three to seven harmonics are evident in first half of each note; the three lowest harmonics are about equal in intensity and the pitch at the beginning of each is 0.70–0.90 (\bar{x} = 0.82), 1.12–1.35 (\bar{x} = 1.25), and 1.64–1.80 (\bar{x} = 1.71) kHz. Each of these harmonics declines about one third of its pitch in the dura-

tion of the note. The fifth or six harmonic beginning at 2.42–2.49 (\bar{x} = 2.46) or 2.80–2.87 (\bar{x} = 2.84) kHz also declines in pitch and is attenuated.

Stefan Gorzula has informed me (in litt., 16 March 1996) that he examined the holotype (BM 1947.2.18.28) of *Paludicola fischeri* Boulenger, 1890, and thinks that *Physalaemus enesefae* is the same species, which would be known as *Physalaemus fischeri* (Boulenger, 1890). A manuscript on the *Physalaemus* of Venezuela is in preparation by Gorzula, Señaris, and Ayarzagüena.

Physalaemus pustulosus (Cope, 1864)

Material: Km 13, KU 166584–98, 167804 (tadpoles), 167805 (young).

On the night of 15 July 1974, males were calling from muddy pools in the forest and amplexant pairs were on a muddy road at Km 13. The species also is known from Km 38 (Heatwole et al., 1965). Ten males and five females have SVLs of 26.528.9 (\bar{x} = 27.4) and 29.5–32.3 (\bar{x} = 31.1), respectively. In life, the dorsum was dull grayish brown with dark brown markings; the upper arms were orange-tan in some individuals. The venter was grayish white with black flecks or mottling, and the vocal sac was gray; the iris was pale bronze.

Tadpoles and metamorphosing young were obtained from a muddy pool on 26 July 1974. Six tadpoles in Stage 31 have body lengths of 8.2–9.2 (\bar{x} = 8.5) and tail lengths of 20.6–24.7 (\bar{x} = 22.8). Two recently metamorphosed young have SVLs of 8.2 and 9.7. In life, the tadpoles had a grayish-brown dorsum and a grayish-cream belly with a silvery tint; the tail was tan with grayish-brown flecks, and the iris was bronze.

These adults were included in the analysis of geographic variation in skin texture and coloration in *Physalaemus pustulosus* by Cannatella and Duellman (1984). The 15 adults have the following coded states (Cannatella and Duellman, 1984:913): Dorsal color pattern: Code O 6 $\sigma\sigma$; Code 2, 3 $\sigma\sigma$, 5 $\sigma\sigma$; Code 3, 1 σ . Ventral color pattern: Code 0, 8 $\sigma\sigma$, 5 $\sigma\sigma$; Code 1, 2 $\sigma\sigma$. Dorsal pustules: Code 2, 5 $\sigma\sigma$; Code 3, 10 $\sigma\sigma$.

MICROHYLIDAE

Ctenophryne geayi Mocquard, 1904

Material: Km 13, KU 167374–84, 167777 (C&S).

After 45 mm of rain in the early evening of 26 July 1974 at Km 13, males were calling from beneath dead leaves in, or at the edge of, water in a flooded depression in the forest. Eleven males have SVLs of 31.9–41.1 (\bar{x} = 35.9) and one gravid female, 46.8. In life, the dorsum was dark chocolate-brown with a white middorsal stripe and white flecks dorsolaterally; the flanks and anterior and posterior surfaces of the thighs were dark brown. The fingers, toes, and venter were dark brown with white spots, and the vocal sac was dark grayish brown; the iris was grayish bronze.

The call consists of a coarse trill. Analysis of two recordings (KU Tapes 1322–23 of one individual not collected and KU 167374 having a SVL of 32.0) made at 22°C at Km 13 and containing five calls reveals the following param-

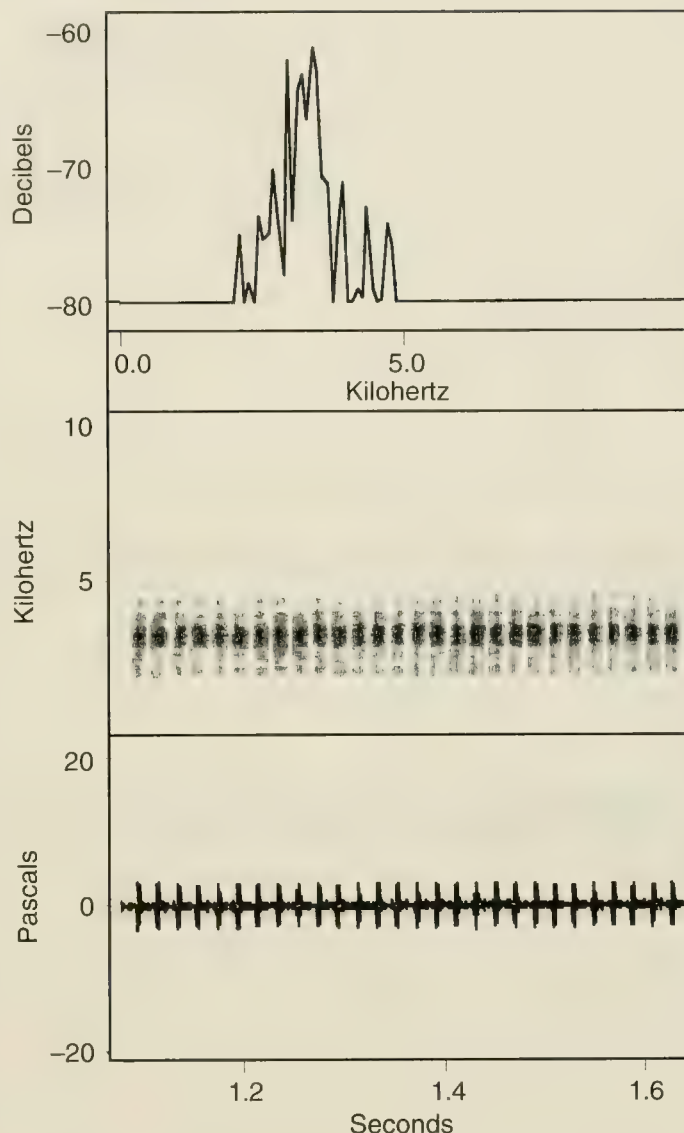


Fig. 25. Spectrum, spectrogram, and waveform of part of advertisement call of *Ctenophryne geayi*, KU Tape 1323, Note 1. Recorded at 22°C; sampling frequency 22.3 kHz.

eters (Fig. 25): notes per call group 1, note repetition rate about 3 notes/min, duration of notes 6.0–7.2 (\bar{x} = 6.3) sec; pulse rate 43–55 (\bar{x} = 47.4) pulses/sec. Notes expand about 3 kHz between 2 and 5 kHz, with two or three frequencies of about equal intensity. Among three notes on KU Tape 1322, the dominant frequencies are at 2.30, 2.64, and 2.98 kHz in Note 1, at 2.37 and 2.80 kHz in Note 2, and at 2.61 kHz in Note 3. In two notes on Tape 1323, the dominant frequencies are at 2.99, 3.21, and 3.39 kHz in Note 1 and at 3.39 and 3.73 in Note 2.

These specimens were included in a study of geographic variation in *Ctenophryne geayi* by Zweifel and Myers (1989), who illustrated the ventral color patterns of six of the specimens and referred these specimens to the "northern (and western) pattern type." Zweifel and Myers

(1989) commented on differences in recordings of calls of *C. geayi* from 20 km SW San José de Guaviare, Vaupés, Colombia (Nelson, 1973) and from Panguana, Departamento Huánuco, Peru (Schlüter, 1980). Both of these calls have lower dominant frequencies—1.1–1.3 kHz in the former and 0.5–0.1 kHz in the latter—than the calls from Km 13. The pulse rates are on the average 39.9 pulses/sec in the calls from Colombia recorded at 27.7°C and 44.5 pulses/sec in the calls from Peru recorded at 23°C. Thus, the calls of the Peruvian and Venezuelan frogs are nearly identical despite differences in dominant frequencies.

Elachistocleis bicolor (Valenciennes, 1838)

Material: Km 13, KU 167388–408, 167778–79 (C&S).

On 26 July 1974 at Km 13, males were calling from water up to 30 cm in depth in flooded forest. Most calling individuals held the forelimbs straight down on floating sticks or leaves; the back was arched with the snout pointing upwards. The SVLs of 21 males are 26.5–31.8 (\bar{x} = 29.6). In life, the dorsum was grayish brown with or without a narrow, cream middorsal line; the stripe on the posterior surface of the thigh, and the spots in the groin, on the anterior surface of the thigh, and on the inner surface of the shank were orange. The belly and ventral surfaces of thighs were creamy yellow, and the vocal sac was dark gray; the iris was pale brown (Fig. 11).

The taxonomy of *Elachistocleis* is chaotic. Dunn (1949) applied the name *Elachistocleis bicolor* (Valenciennes, 1838) to frogs having an immaculate venter and the name *E. ovalis* (Schneider, 1799) to frogs having a dark venter with small pale spots. For frogs from Trinidad, Kenny (1969) used the name *E. surinamensis* (Daudin, 1802); these frogs are large and have dark venters with pale spots. See Frost (1985) for further comments. *Elachistocleis bicolor* apparently is the only available name for *Elachistocleis* having an immaculate venter; thus, the name is applied to the frogs from Km 13.

Elachistocleis species

Material: Km 144, KU 167409–28, 167780–81 (C&S).

On 17 July 1974, a male was under a termite nest by day, and another male was calling from beneath the roots of a plant in mud adjacent to a temporary pond. On 22 July, males were calling from beneath clumps of dead grass, beneath leaves, and in depressions in the muddy bank of the same pond, as well as in shallow water near the edge of the pond. One female was on the bank of the pond, and amplexant pairs were on the bank and in shallow water. One male was being engulfed by a colubrid snake, *Liophis zweifeli*, at night. Fifteen males have SVLs of 29.7–34.3 (\bar{x} = 32.2), and seven gravid females have SVLs of 38.0–44.0 (\bar{x} = 41.5). In life, the dorsum was brownish black to black with bluish-gray flecks; the venter was black with bluish-gray flecks. The spots on the chest, in the groin, and on the ventral surfaces of the limbs were yellow, whereas the spots in the inguinal region, on the inner surfaces of the shanks, and on the anterior and posterior surfaces of the thighs were bright orange; the iris was pale gray (Fig. 11).

The advertisement call consists of a loud buzz. Analysis of two recordings containing seven notes (KU Tapes 1326–27, KU 167411–12, SVLs 31.7 and 34.0, respectively) made at 16.5°C at Km 144 reveal the following parameters (Fig. 26): notes per call group 1, intervals between notes 11–20 (\bar{x} = 14.2) sec, duration of notes 2.29–4.59 (\bar{x} = 3.78) sec, pulse rate 130–142 (\bar{x} = 136) pulses/sec, dominant frequency 3.07–3.39 (\bar{x} = 3.23) kHz.

Because of the taxonomic confusion within *Elachistocleis* (Frost, 1985), I am unwilling to assign the frogs from the Gran Sabana to any named species. Instead I provide comparisons with, and comments on, three taxa—*E. surinamensis* (Daudin), *E. ovalis* (Schneider), and *Relictivomer pearsei* (Ruthven)—from northern South America that might be confused with the frogs from Gran Sabana.

Elachistocleis surinamensis was described from “Suriname” and was considered to be a synonym of *E. ovalis* by Parker (1934). However, Kenny (1969) recognized *E. surinamensis* as a distinct species, which is known from Suriname and Trinidad (Frost, 1985). According to Kenny’s (1969:67) description of *Elachistocleis surinamensis* from Trinidad, that species is the same size as those from the Gran Sabana but differs by having a “...very thin black vertebral line...” and “Belly and underparts deep yellow with brown marbling, mottling or reticulations....” The frogs from the Gran Sabana lack a black vertebral line and apparently have more dark pigment on the venter, so that the belly appears to be dark with pale yellow spots.

The holotype of *Elachistocleis ovalis* is unknown and of unknown provenance. The species is reported to have a wide range from Panama and Colombia southward east of the Andes to Argentina. Dunn (1949:12) applied this name to frogs that he defined as “... a small species with a dark belly with light dots, with a broad stripe on the thigh, and with inguinal spots ...” Small ($\sigma\sigma$ 24–27, ♀♀ 29–30) *Elachistocleis* having spotted venters from savannas in Venezuela and Suriname were referred to *E. ovalis* by Hoogmoed and Gorzula (1979). These frogs, which are smaller than those from the Gran Sabana were described as: “In life, the spots in axils, groins, hollow of the knee and on the back of the thigh orange; belly marbled lemon yellow and gray” (Hoogmoed and Gorzula, 1979:204).

Relictivomer pearsei was described from Fundación, Colombia. This species has been reported only from northern Colombia and Panama (Dunn, 1949; Cochran and Goin, 1970). According to Carvalho (1954), *Relictivomer* differs from *Elachistocleis* by having small posterior vomers; this observation was made on specimens from Fundación, Departamento Magdalena, Colombia. The Gran Sabana is more than 1000 km ESE of the easternmost localities of *R. pearsei* in departamentos Magdalena and Norte de Santander, Colombia (Cochran and Goin, 1970). Yet, superficially, the specimens from the Gran Sabana closely resemble *R. pearsei*. Comparison of the specimens from the Gran Sabana with eight from Panama (KU 77577–79, 108915–17, 116502–03) reveals no noticeable external struc-

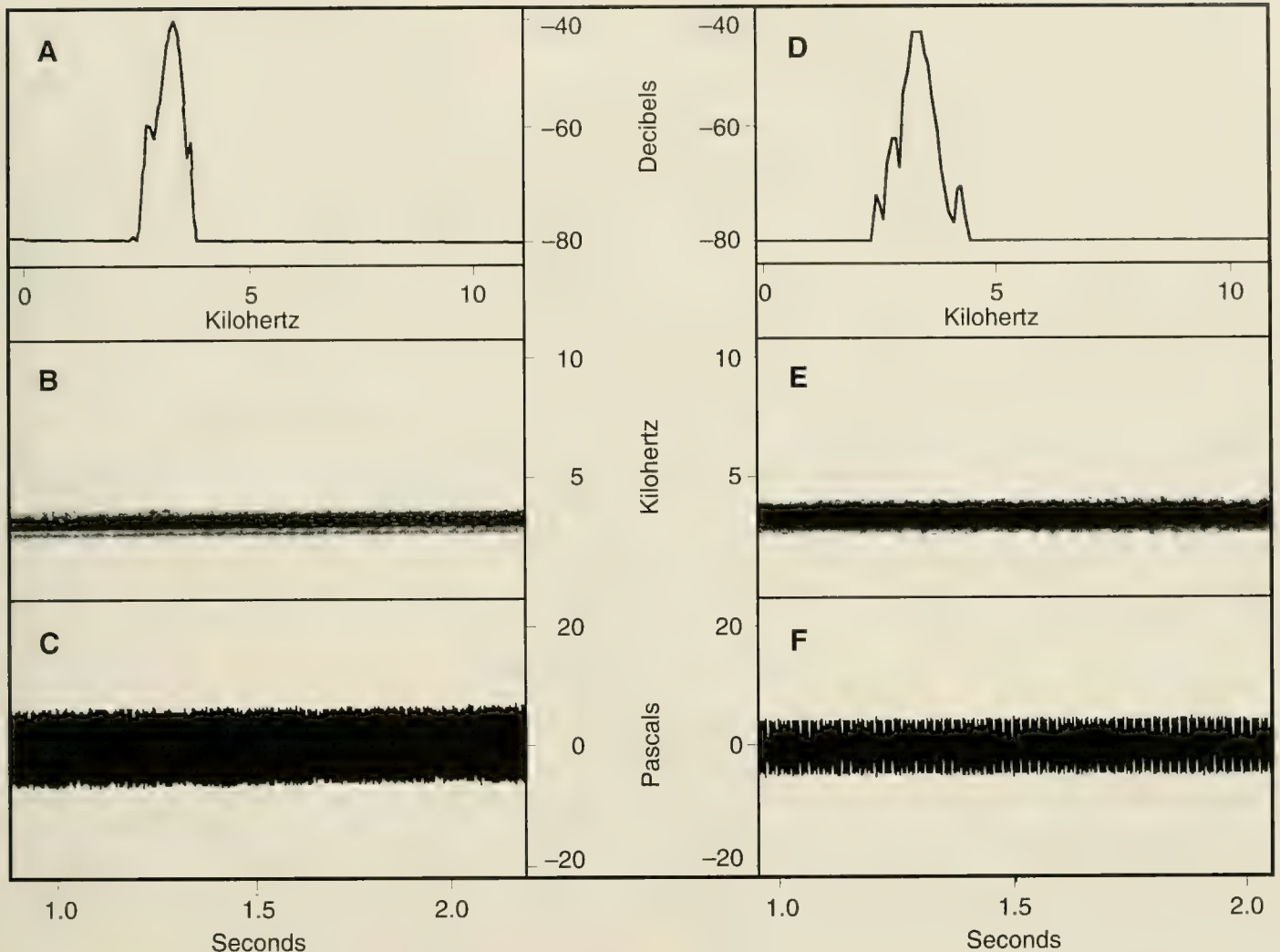


Fig. 26. Spectrums, spectrograms, and waveforms of parts of advertisement calls of microhylid frogs, sampling frequency 22.3 kHz. A–C: *Elachistocleis* sp., KU Tape 1326, Note 4, Km 144, Bolívar, Venezuela, recorded at 16.5°C. D–F: *Relictivomer pearsei*, KU Tape 321, Note 3, Cerro La Campana, Panama, Panama, recorded at 23°C.

tural differences, except that the Panamanian specimens are slightly smaller in SVL—six males 29.4–33.6 (\bar{x} = 32.5) and two females 36.3 and 37.2. Moreover, the coloration is essentially the same, except that the ventral pattern is less bold in Panamanian specimens; frogs both from Panama and the Gran Sabana have orange spots in the inguinal region.

Analysis of one recording of *Relictivomer pearsei* containing three notes (KU Tape 321, KU 77577, SVL 34.9) made at 23°C on the S slope of Cerro La Campana, Panama Province, Panama, reveals the following parameters (Fig. 26): notes per call group 1, intervals between notes 14–18 (\bar{x} = 16) sec, duration of notes 2.28–4.57 (\bar{x} = 3.64) sec, pulse rate 155–160 (\bar{x} = 157) pulses/sec, dominant frequency 3.05–3.39 (\bar{x} = 3.28) kHz. The notes produced by Venezuelan and Panamanian frogs are nearly identical except for

pulse rate; the higher pulse rate is expected in the Panamanian recording made at 23°C compared with the Venezuelan recordings made at 16.5°C.

The similarities in external structure, coloration, and advertisement calls of specimens from Panama and the Gran Sabana suggest that they might be conspecific, even though a gap of more than 1000 km exists between the closest localities. However, *R. pearsei* has small posterior vomers. Examination of two cleared-and-stained adult females (KU 167780–81) from the Gran Sabana reveals that they are like *Elachistocleis* in characters analyzed by Zweifel (1986) and Wild (1995) in having (1) small, crescent-shaped, proximal clavicles about one-fourth the length of the coracoids, (2) maxillae not in contact with quadratojugals, (3) alary processes of premaxillae inclined anteriorly and shelf of premaxillae not indented, (4) anterior vomers present,

and (5) posterior vomers and neopalatines absent.

Clearly, the status of various populations of *Elachistocleis* and the generic status of *Relictivomer* are highly questionable. The ontogenetic ossification of vomers must be understood in order to justify the generic recognition of *Relictivomer*. Thus, it is not possible to assign the specimens from the Gran Sabana to a known taxon. They might represent a vicariant population related to *R. pearsei* or an undescribed species of *Elachistocleis*.

Otophryne robusta Boulenger, 1900

Material: Km 120, RMNH 27245–46 (tadpoles).

Three tadpoles were amidst leaves in a slowly flowing, tannin-colored stream on sandy substrate on 16 May 1978; another was collected at the same site on 10 June 1978. Two of the original tadpoles were taken alive to The Netherlands and maintained in an aquarium; they died and subsequently were lost. The distinctive tadpoles of this diurnal species were described by Wassersug and Pyburn (1987). In life (RMNH 27245), the dorsal surface of body was olive with gray-brown spots and a small red spot in front of eye; the belly was opaque white, and the tail had a black stripe at the base of the upper fin.

PIPIDAE

Pipa arrabali Izecksohn, 1976

Material: Km 112, KU 167436, 167437 (skeleton), 167438–39, 167440 (C&S), 167441–49, 167450 (C&S).

Adults, subadults, and juveniles were found in muddy roadside ditches and puddles by day and night. Some were feeding on tadpoles of *Hyla minuta* and *Leptodactylus longirostris*. Eleven individuals are juveniles and subadults having SVLs of 20.8–35.1 (\bar{x} = 29.0). Two brooding females have SVLs of 40.2 and 40.6. In life, the dorsum was dull brown with darker brown spots; venter was orange-brown with dark brown spots, and the iris was black.

RANIDAE

Rana palmipes Spix, 1824

Material: Km 90, RMNH 27261.

An adult female having a SVL of 125 was dead on the road on the night of 11 June 1978 at Km 90. The ventral surfaces of the limbs were heavily mottled with black and cream; the anterior and posterior surfaces of the thighs were black with cream lines and reticulations. The species was reported from Km 77 by Heatwole et al. (1965).

ANURAN COMMUNITIES

Sufficient data are available for the assemblages of anurans at one site in the humid tropical forest, two sites in the very humid lower montane forest on the north slope of the Sierra de Lema, and in savanna on the Gran Sabana to assess community composition and structure with respect to sizes of frogs and microhabitat utilization, at least by calling males.⁴ Unless specified otherwise, the data refer only to adult males; measurements refer only to specimens from the site under discussion. Except for a few species, no information is available on seasonal differences, and no precise data are available on abundance, which thus must be estimated from the numbers of individuals collected.

HUMID TROPICAL FOREST

Among the 27 species of anurans known from the Río Cuyuni site, the calling sites of six species are in water, seven on land, 11 on bushes (1 also on land), and four in trees. Considerable differences in sizes of frogs, as measured by SVL, are evident among the four microhabitats (Fig. 27). Two small species, *Epipedobates femoralis* and *Adenomera hylaedactyla*, are terrestrial and call by day, although activity in *Adenomera* seems to be restricted to late afternoon. Excluding these two diurnal species, the smallest species call from bushes usually no more than 1.5 m above the ground or surface of the water in ponds; the ranges of mean SVLs of 11 such species are 20.0 (*Hyla*

minuscula) to 66.1 (*Hyla geographicala*) (\bar{x} = 30.9). Six species that call from water in ponds are slightly larger; the ranges of mean SVLs are 27.0 (*Physalaemus enesefae*) to 64.4 (*Osteocephalus taurinus*) (\bar{x} = 37.6). Although the largest species call from land, several smaller species also are in the same macrohabitat, and the range of mean SVLs of five nocturnal species are 32.4 (*Scinax rubra*) to 138.3 (*Leptodactylus pentadactylus*) (\bar{x} = 73.4). As a group, the four species that call from tree limbs have mean SVLs from 81.0 (*Phrynohyas venulosa*) to 97.4 (*Hyla boans*).

Of the 27 species at the Río Cuyuni site, 22 were found at edges of ponds at night; these species occupied microhabitats ranging from bare ground and water to tree limbs more than 5 m above the ground, and *Adenomera hylaedactyla* called from land away from water (Fig. 28). However, different ponds contained different assemblages of species. For example, small, shallow puddles that seemed to be the preferred calling sites of *Physalaemus pustulosus* were occupied by only two other species, *Hyla crepitans* and *H. minuta*. The latter species was by far the most abundant anuran on the night of 26 July 1974, when an estimated several thousand males were calling from every body of water. It was the only species that occurred with all other pond breeding anurans at the site; likewise, *Phyllomedusa hypochondrialis* occurred at the same ponds of all species except the shallow puddles inhabited by *Physalaemus pustulosus*.

Co-occurrence of species in ponds was variable (Table 5). For example, 11 species were encountered in and around a deep pond in forest that had nearly a complete canopy. Among these 11 species, *Leptodactylus pentadactylus* was

⁴ This "snapshot" approach (Duellman and Pianka, 1990) has severe limitations. Data presented here are not meant to define community organization but simply to show differences among breeding assemblages of frogs at specific times.

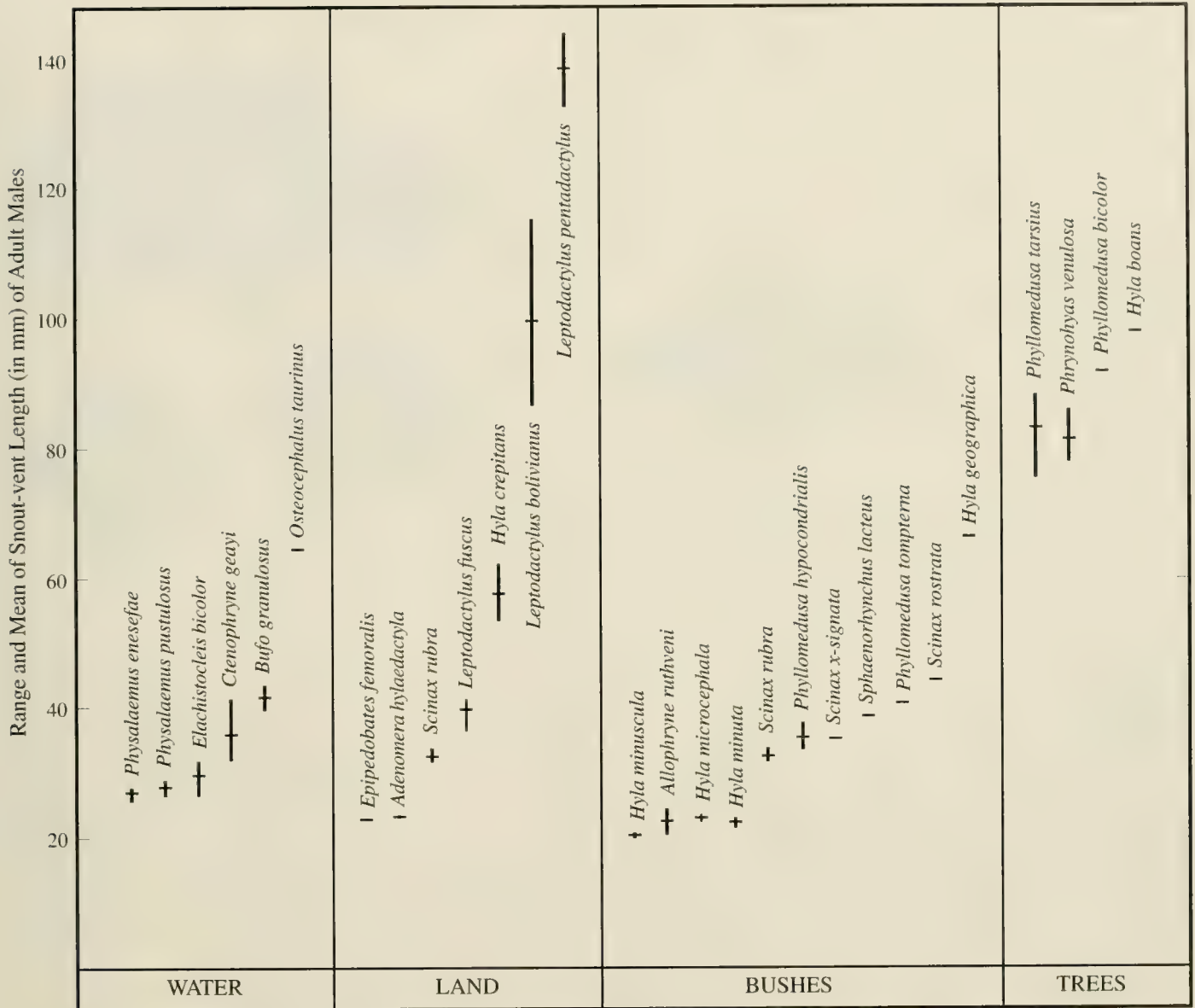


Fig. 27. Snout-vent lengths of adult males of 27 species of anurans with respect to perching and calling sites at 13 km S and 1 km E of the Río Cuyuni bridge, Estado Bolívar, Venezuela. Vertical bars = range; horizontal lines = mean. *Adenomera hylaedactyla* and *Epipedobates femoralis* are diurnal; all others are nocturnal.

on land at the edge of the water, as were some *Scinax rubra*; others of the latter species were on low vegetation in, or at the edge of the water, a microhabitat also utilized by *Allophryne ruthveni*, *Hyla geographica*, *H. minuta*, and *Phyllomedusa hypocondrialis*. The only species calling from limbs of trees was *Phrynohyas venulosa*. All other species were in the water—*Physalaemus enesefae* and *Ctenophryne geayi* under leaves or logs, or in cavities, at the edge of the pond; *Elachistocleis bicolor* were holding onto grasses or debris in the water, and *Osteocephalus taurinus* were floating on the surface before swimming to shore in an effort to escape. With the exception of *Hyla geographica* represented by one individual, all species were abundant at the pond.

Other ponds in the forest had different assemblages of species. One of these contained only seven species, including the ubiquitous *Hyla minuta* and *Phyllomedusa hypocondrialis*, together with *Hyla microcephala* calling from bushes and two species (*Phyllomedusa bicolor* and *P. tarsius*) calling from branches over water. *Hyla crepitans* was on the ground at the edge of the pond, where one *Phyllomedusa tompeterna* was on a *Heliconia* leaf.

The two smallest *Hyla* (*H. microcephala* and *H. minuscula*) called from the same types of low perches above water, but they were not found in the same ponds. Likewise, *Leptodactylus pentadactylus* and *L. bolivianus* were not in the same ponds, and the two species of *Physalaemus* (*P.*

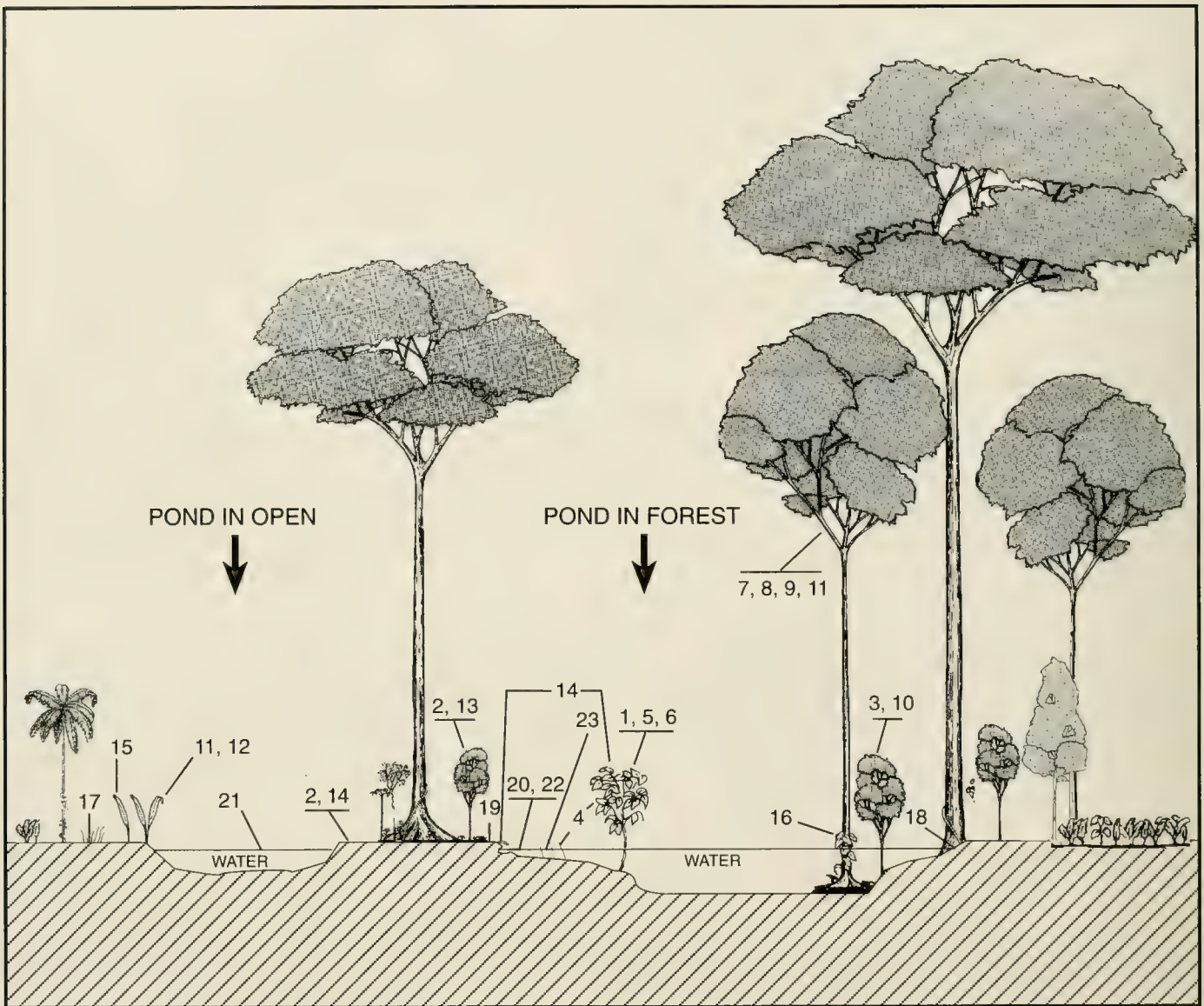


Fig. 28. Profiles of temporary ponds at site 13 km S, 1 km E Cuyuni, Departamento Bolívar, Venezuela, showing vegetation structure and perching or calling sites of 23 species of anurans: 1 = *Allophryne ruthveni*; 2 = *H. crepitans*; 3 = *H. geographica*; 4 = *H. microcephala*; 5 = *H. minuscula*; 6 = *H. minuta*; 7 = *Osteocephalus taurinus*; 8 = *Phrynohyas venulosa*; 9 = *Phyllomedusa bicolor*; 10 = *P. hypocondrialis*; 11 = *P. tarsius*; 12 = *P. tomopterna*; 13 = *Scinax rostrata*; 14 = *S. rubra*; 15 = *S. x-signata*; 16 = *Sphaenorhynchus lacteus*; 17 = *Adenomera hylaedactyla*; 18 = *Leptodactylus bolivianus*; 19 = *L. pentadactylus*; 20 = *Physalaemus enesefae*; 21 = *P. pustulosus*; 22 = *Ctenophryne geayi*; 23 = *Elachistocleis bicolor*.

enesefae and *P. pustulosus*) were not calling from the same bodies of water. Co-occurrence was highest in *Hyla minuta* with 20 other species, *Phyllomedusa hypocondrialis* (19), and *Leptodactylus pentadactylus* (16), and lowest in *Hyla microcephala* (3), *Scinax x-signata* (3), and *Physalaemus pustulosus* (2).

The deep forest pond having an assemblage of 11 species was the only pond where *Allophryne ruthveni*, *Hyla geographica*, *Ctenophryne geayi*, and *Elachistocleis bicolor* were calling. Likewise, *Sphaenorhynchus lacteus* was heard only in one forest pond. *Phyllomedusa bicolor*, *P. tomopterna*, and

Scinax rostrata are represented only by one observation each, so it is likely that more data would expand their co-occurrence with other species. Scattered males of *Hyla boans* were calling from trees throughout the forest, but they were not congregated for breeding.

These data suggest that although as many as 23 species may be calling in one area on a given night, individual ponds are utilized by different combinations of species. In some cases it is clear why species are absent in a pond. For example, the absence of partially submerged ground cover seems to be necessary for the occurrence of *Physalaemus*

Table 5. Microsympatry (occurrence in same pond) of nocturnally calling species of male anurans at breeding ponds 13 km S and 1 km E of Puente Cuyuni. Abbreviations for names of species in headings of columns are given in parentheses after the name in the first column. + = occurrence in same pond.

| SPECIES | ARU | HCR | HGE | HMC | HMI | HMN | OTA | PVE | PBI | PHY | PTA | PTO | SLA | SRO | SRU | SXS | LBO | LPE | PEN | PTU | CGE | EBI |
|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| <i>Allophryne ruthveni</i> (ARU) | • | - | + | - | - | + | + | + | - | + | - | - | - | - | + | - | - | + | + | - | + | + |
| <i>Hyla crepitans</i> (HCR) | - | • | - | + | - | + | - | - | + | + | + | + | - | + | + | - | + | + | + | + | - | - |
| <i>Hyla geographica</i> (HGE) | + | - | • | - | - | + | + | + | - | + | - | - | - | - | + | - | - | + | + | - | + | + |
| <i>Hyla microcephala</i> (HMC) | - | + | - | • | - | + | + | - | + | + | + | + | - | - | + | - | - | + | + | - | - | - |
| <i>Hyla minuscula</i> (HMI) | - | - | - | - | • | + | - | - | - | + | - | - | - | - | - | - | - | + | - | - | - | - |
| <i>Hyla minuta</i> (HMN) | + | + | + | + | + | • | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| <i>Osteocephalus taurinus</i> (OTA) | + | - | + | + | - | + | • | + | - | + | + | - | - | - | + | - | + | + | + | - | + | + |
| <i>Phrynohyas venulosa</i> (PVE) | + | - | + | - | - | + | + | • | - | + | - | - | - | - | + | - | + | + | + | - | + | + |
| <i>Phyllomedusa bicolor</i> (PBI) | - | + | - | + | - | + | + | - | • | + | + | + | + | + | + | - | + | + | + | - | + | + |
| <i>Phyllomedusa hypochondrialis</i> (PHY) | + | + | + | + | + | + | + | + | + | • | + | + | + | + | + | + | + | + | + | - | + | + |
| <i>Phyllomedusa tarsius</i> (PTA) | - | + | - | + | - | + | + | - | + | + | + | • | - | + | - | - | + | + | + | - | - | - |
| <i>Phyllomedusa tomodoterna</i> (PTO) | - | + | - | + | - | + | + | - | + | + | + | - | - | - | + | - | - | + | + | - | - | - |
| <i>Sphaenorhynchus lacteus</i> (SLA) | - | + | - | + | - | + | + | - | - | + | - | - | • | - | + | - | - | + | + | - | - | - |
| <i>Scinax rostrata</i> (SRO) | - | + | - | - | - | + | + | - | - | + | + | - | - | • | - | - | - | + | + | - | - | - |
| <i>Scinax rubra</i> (SRU) | + | + | + | - | - | + | + | + | - | + | + | - | + | - | • | - | + | + | + | - | + | + |
| <i>Scinax x-signata</i> (SXS) | - | - | - | - | - | + | + | - | - | + | - | - | - | - | - | • | - | + | + | - | - | - |
| <i>Leptodactylus bolivianus</i> (LBO) | - | + | - | - | - | + | + | + | - | + | + | - | - | - | + | - | • | - | + | - | - | - |
| <i>Leptodactylus pentadactylus</i> (LPE) | + | + | + | + | + | + | + | + | - | + | + | - | + | + | + | + | - | • | + | - | + | + |
| <i>Physalaemus ensefae</i> (PEN) | + | + | + | + | - | + | + | + | - | + | + | - | - | + | + | - | + | + | • | - | + | + |
| <i>Physalaemus pustulosus</i> (PTU) | - | + | - | - | - | + | - | - | - | - | - | - | - | - | - | - | - | - | - | • | - | - |
| <i>Ctenophryne geayi</i> (CGE) | + | - | + | - | - | + | + | + | - | + | - | - | - | - | + | - | - | + | + | - | • | + |
| <i>Elachistocleis bicolor</i> (EBI) | + | - | + | - | - | + | + | + | - | + | - | - | - | - | + | - | - | + | + | - | + | • |
| Total | 10 | 12 | 9 | 10 | 3 | 21 | 13 | 11 | 6 | 20 | 11 | 6 | 4 | 6 | 14 | 3 | 8 | 17 | 15 | 2 | 10 | 10 |

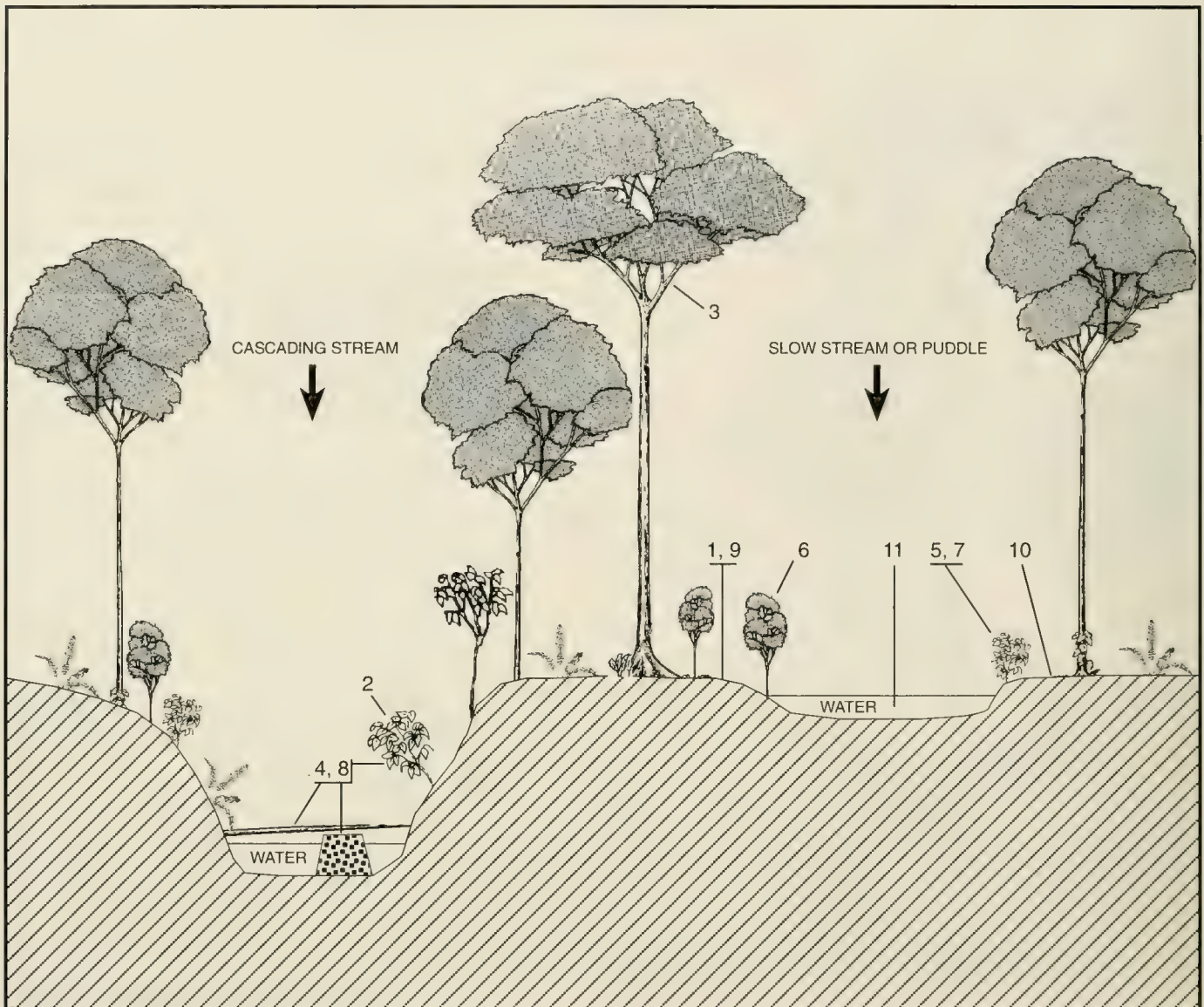


Fig. 29. Profiles of streams at Km 112 on the El Dorado-Santa Elena de Uairén Road, Estado Bolívar, Venezuela, showing vegetation structure and perching and calling sites of 11 species of anurans: 1 = *Bufo guttatus*; 2 = *Hyalinobatrachium orientale*; 3 = *Hyla boans*; 4 = *H. lemai*; 5 = *H. minuta*; 6 = *H. multifasciata*; 7 = *H. sibleszi*; 8 = *Stefania evansi*; 9 = *Leptodactylus longirostris*; 10 = *L. rugosus*; 11 = *Pipa arrabali*.

enesefae and *Ctenophryne geayi*, and trees provide essential perches for *Phyllomedusa bicolor* and *P. tarsius*; yet neither species was present at the canopy-covered, deep pond in the forest. Advertisement calls have been considered to be important premating isolating mechanisms in anurans (Duellman, 1967); however, the three small species of *Hyla* (*H. microcephala*, *minuscule*, and *minuta*) utilizing the same structural calling sites have similar calls, and the four species of *Phyllomedusa*, all of which have similar calls (albeit with different intensities) but call from various heights above the water, were found in the same pond. How many of these differences are random and how many are depen-

dent upon unknown factors cannot be ascertained from observations on two nights.

VERY HUMID LOWER MONTANE FOREST

Among the 16 species studied in sites in cloud forest at Km 112 and Km 127 on the El Dorado-Santa Elena de Uairén Road, only one species, *Colostethus parkerae*, is diurnal. Of the 15 nocturnal species, four species call from the ground, one from water, eight from vegetation over water, and two from vegetation away from water (Figs. 29, 30). Differences in size, as measured by SVL exist among the four microhabitats (Fig. 31). The range of mean SVLs

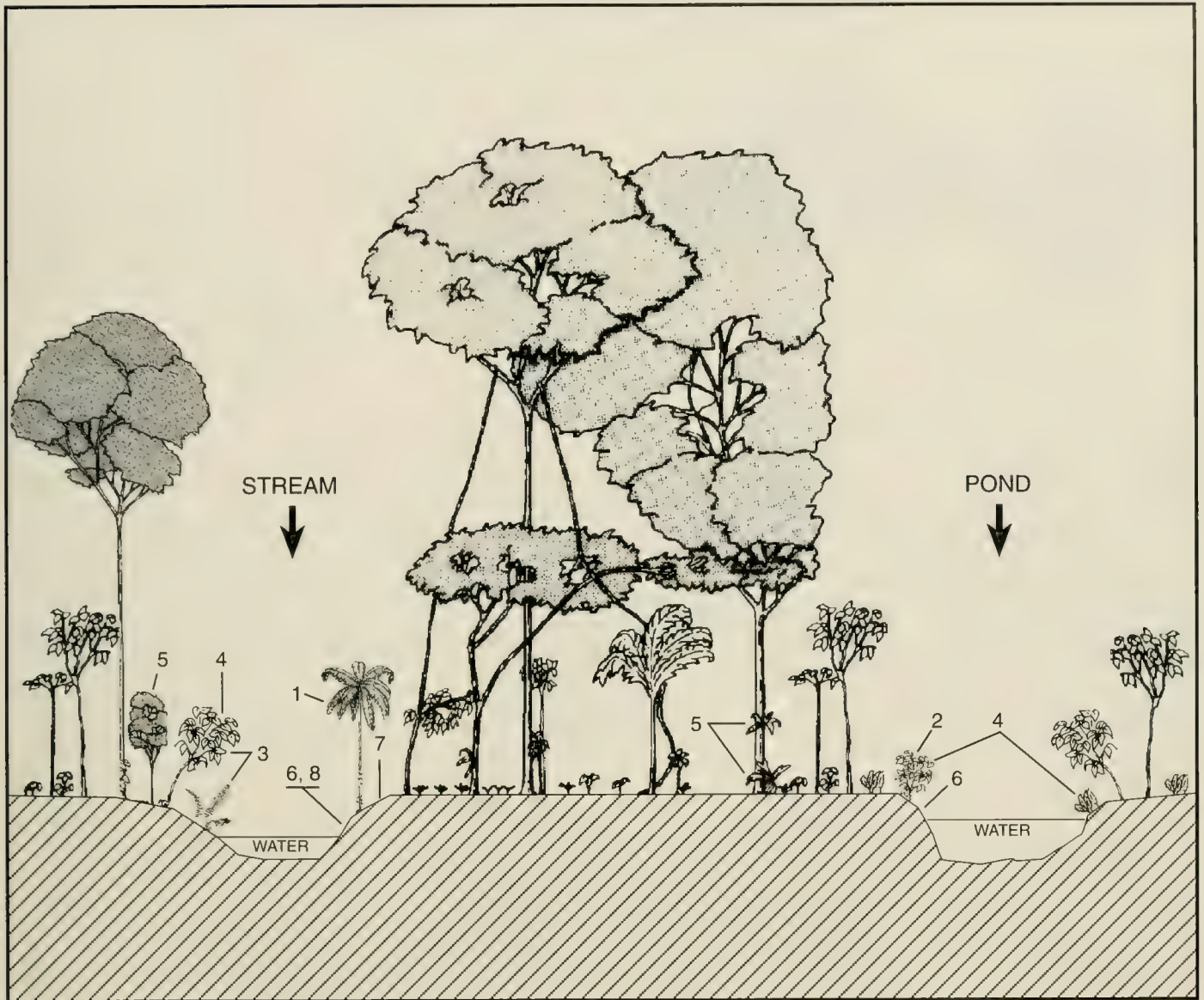


Fig. 30. Profiles of stream and pond at KM 127 on El Dorado–Santa Elena de Uairén road, Estado Bolívar, Venezuela, showing vegetation structure and perching or calling sites of eight species of anurans: 1 = *Centrolene* sp., 2 = *Hyla minuta*, 3 = *H. sibleszi*, 4 = *Scinax danae*, 5 = *Eleutherodactylus pulvinatus*, 6 = *Leptodactylus longirostris*, 7 = *L. rugosus*, 8 = *L. sabanensis*.

of the four species that call from the ground is 37.8 (*Leptodactylus longirostris*) to 120.0 (*Bufo guttatus*). The mean SVL of *Pipa arrabali*, the only species that calls from water, is 40.4. Of the species associated with herbs and bushes over streams, the range of mean SVLs is 20.8 (*Centrolene* sp.) to 42.3 (*Stefania evansi*), whereas of the species that call from herbaceous vegetation and bushes over ponds, the range of mean SVLs is 22.3 (*Hyla minuta*) to 53.2 (*Hyla multifasciata*). The mean SVL of *Eleutherodactylus pulvinatus*, the only bush inhabitant not associated with ponds or streams is 22.9, and that for the only tree inhabitant, *Hyla boans*, is 86.9.

Four of the species lack aquatic larval stages; *Eleutherodactylus pulvinatus* has direct development of terrestrial eggs, and the eggs of *Stefania evansi* and *Pipa arrabali* undergo direct development on the dorsum (*Stefania*) or imbedded in the dorsum (*Pipa*) of the female; the eggs of *Adelophryne gutturosa* are large and unpigmented and presumably undergo direct development (Ayarzagüena and Diego-Aransay, 1985). The tadpoles of *Bufo guttatus* probably develop in ponds, as do those of *Hyla minuta*. Those of *Centrolene*, *Hyalinobatrachium orientale*, and *Hyla lemai* probably develop in cascading streams, whereas those of *Colostethus parkerae*, *Hyla boans*, *H. sibleszi*, *Leptodactylus*

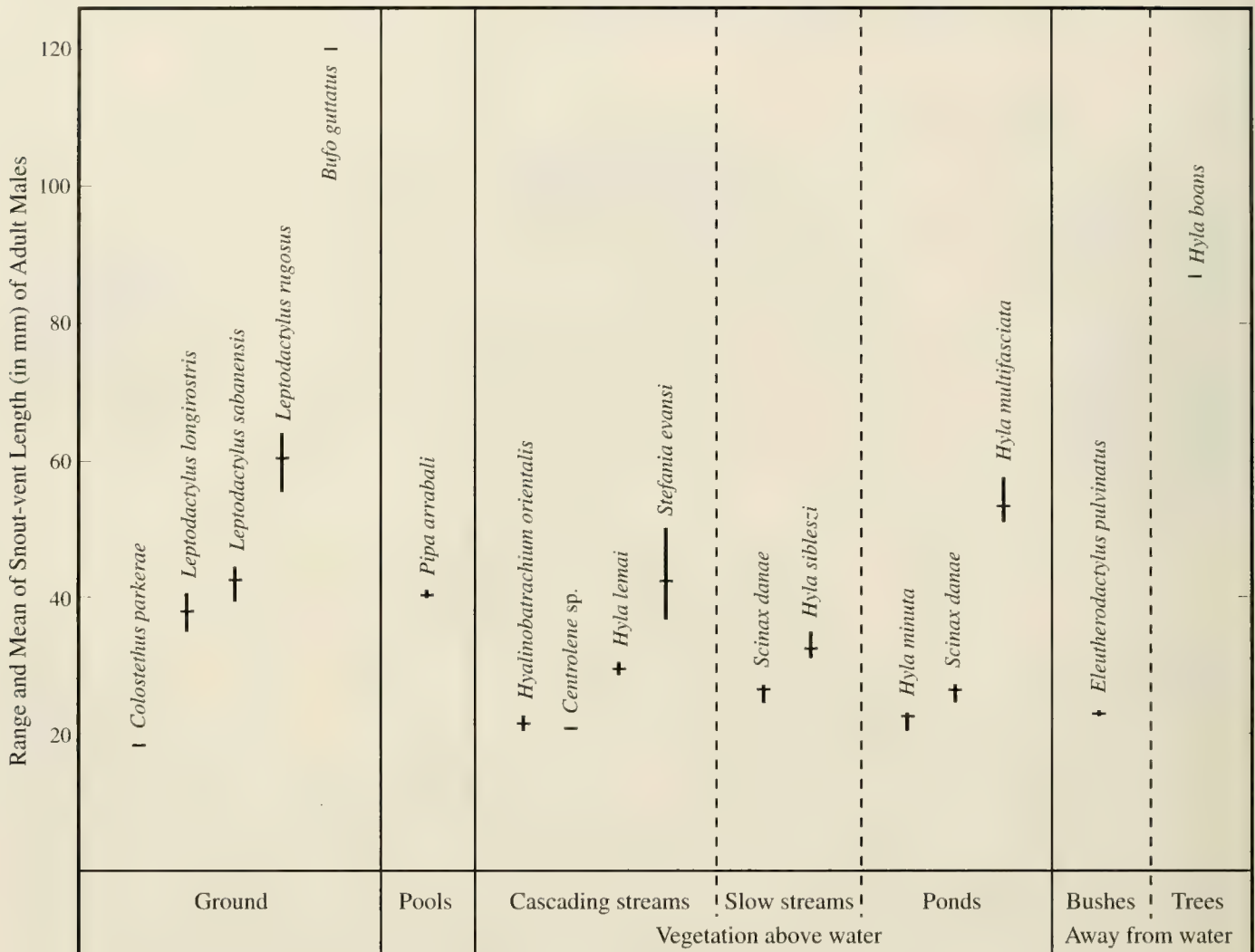


Fig. 31. Snout-vent lengths of adult males of 16 species of anurans with respect to perching and calling sites at Km 112 and Km 127 on the north slope of the Sierra de Lema, Estado Bolívar, Venezuela. Vertical bars = range; horizontal lines = mean. *Colostethus parkerae* is diurnal; all others are nocturnal.

longirostris, *L. sabanensis*, and *Otophryne robusta* develop in slow-moving streams. The tadpoles of *Hyla multifasciata* and *Scinax danae* may develop in ponds or sluggish streams, whereas those of *Leptodactylus rugosus* always seem to be associated with rivulets in granitic rock.

Thus, habitat utilization in the montane forest reflects the size of the frog with respect to calling perches, as it does in the lowland tropical forest. However, specific sites are associated with the aquatic environments in which the tadpoles develop—ponds, slow-moving streams, cascading streams, or rivulets in granitic outcrops.

GRAN SABANA

Two major types of habitats exist on the Gran Sabana—grasslands and gallery forest along streams. All the 14 species in the Gran Sabana are nocturnal. Four species (*Bufo*

marinus, *Hyla minuta*, *Scinax exigua*, and *Leptodactylus sabanensis*) occur in both habitats, and most of the larger treefrogs (e.g., *Hyla boans*, *H. lemai*, *H. multifasciata*, and *H. sibleszi*) apparently are restricted to the gallery forest, but *Hyla crepitans* occurs in the grassland (Fig. 32). The lentic tadpoles of species, such as *Hyla boans* and *Hyla multifasciata*, develop in quiet pools in streams in the dry season.

Differences in size, as measured by SVL exist among the three microhabitats in the grassland and between the grass microhabitat and ground and trees in the gallery forest (Fig. 33). The range of mean SVLs of the four species that call from water in temporary ponds in the grassland is 31.8 (*Tepuihyla rodriguezi*) to 51.3 (*Hyla crepitans*). The range in size of four species that call from land next to these ponds is much greater—22.1 (*Hyla minuta*) to 103.0

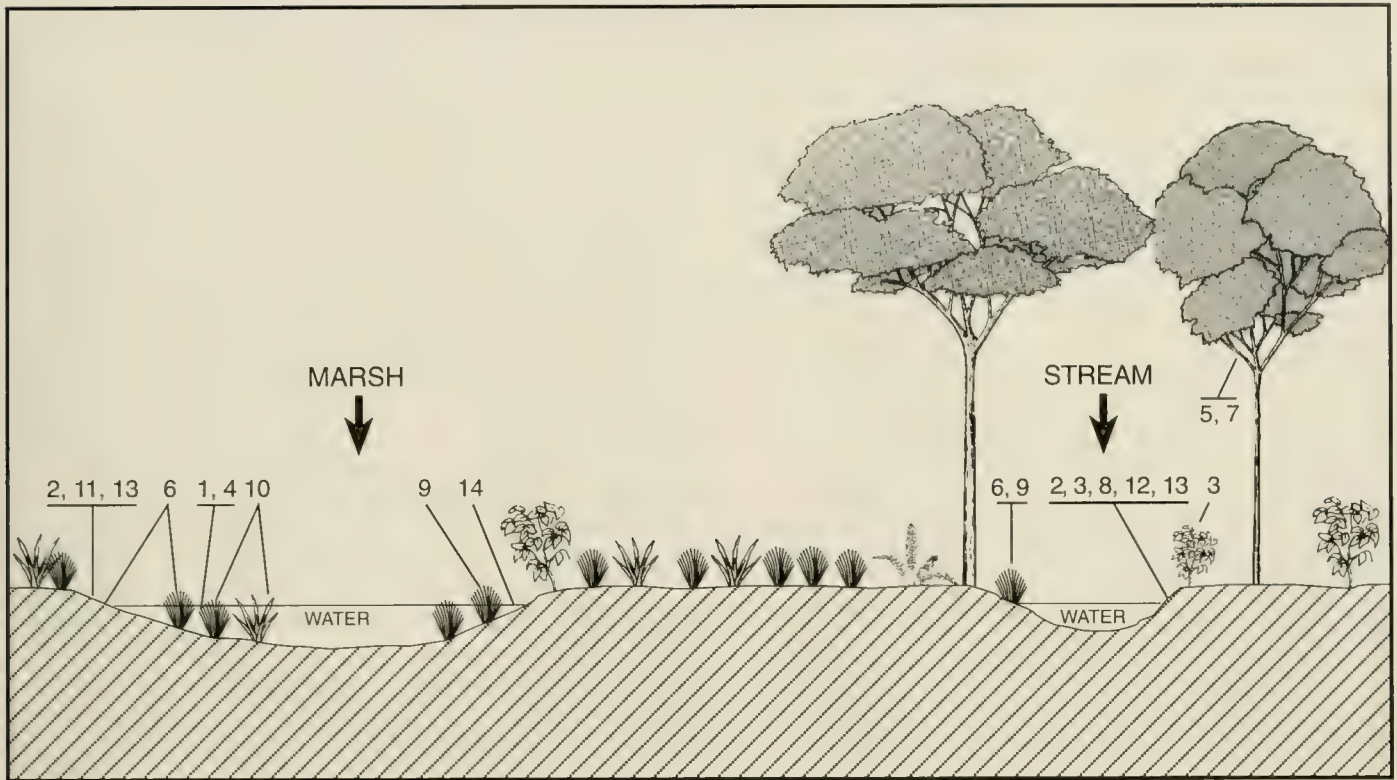


Fig. 32. Profiles of marsh and stream in gallery forest on La Gran Sabana, Estado Bolívar, Venezuela, showing vegetation structure and perching or calling sites of 13 species of anurans: 1 = *Bufo granulosus*; 2 = *Bufo marinus*; 3 = *Hyla boans*; 4 = *H. crepitans*; 5 = *H. lemai*; 6 = *H. minuta*; 7 = *H. multifasciata*; 8 = *H. sibleszi*; 9 = *Scinax exigua*; 10 = *Tepuihyla rodriguezi*; 11 = *Leptodactylus longirostris*; 12 = *L. rugosus*; 13 = *L. sabanensis*; 14 = *Elachistocleis* sp.

(*Bufo marinus*). On the other hand, the smallest species call from grasses in the ponds; the range of means in three species is 19.8 (*Scinax exigua*) to 31.8 (*Tepuihyla rodriguezi*).

Likewise, in the gallery forests, the two smallest species call from low vegetation; these are *Scinax exigua* (\bar{x} = 19.8) and *Hyla minuta* (\bar{x} = 22.1). Five species call from the banks of streams, and the range of mean SVLs is 32.3 (*Hyla sibleszi*) to 103.0 (*Bufo marinus*). The range in mean sizes of species that call from trees is 29.6 (*Hyla lemai*) to 102.9 (*Hyla boans*). *Hyla boans* calls from trees and then descends to the edges of streams to construct nests, where it continues to call.

COMPARISONS

Percentage microhabitat utilization varies between the major types of vegetation (Table 6). In the humid tropical forest and very humid lower montane forest, the greatest number of species calls from bushes and herbaceous vegetation and far fewer call from trees. On the other hand, a higher percentage of species calls from trees in gallery forest in the Gran Sabana, and the absence of trees in the grassland on the Gran Sabana precludes species calling from trees there.

More than 25% of the species in all types of vegetation calls from the ground, and this percentage is highest on

the Gran Sabana, where an equal number of species calls from water in temporary ponds; this percentage is twice that in the humid tropical forest. Only one species, *Pipa arrabali*, calls from water in the very humid lower montane forest.

Most of the species that occur in more than one vegetation type utilize the same microhabitats throughout the different habitats. Thus, *Bufo granulosus* calls from shallow water in temporary ponds in open areas (e.g., road cuts) in the humid tropical forest and in the grasslands of the Gran Sabana; likewise, *Hyla boans* calls from trees in all forested habitats and is absent in the grasslands. Three

Table 6. Percentage of species of male anurans utilizing different microhabitats as calling sites in major vegetation types. Some species use more than one microhabitat.

| Vegetation type | n | Low | | | |
|---------------------------------|----|-------|--------|------------|-------|
| | | Water | Ground | vegetation | Trees |
| Humid tropical forest | 27 | 22.2 | 25.9 | 40.7 | 14.8 |
| Very humid lower montane forest | 16 | 6.1 | 37.5 | 56.3 | 6.1 |
| Gran Sabana (grassland) | 9 | 44.4 | 44.4 | 33.3 | 0.0 |
| Gran Sabana (gallery forest) | 9 | 0.0 | 55.6 | 22.2 | 33.3 |

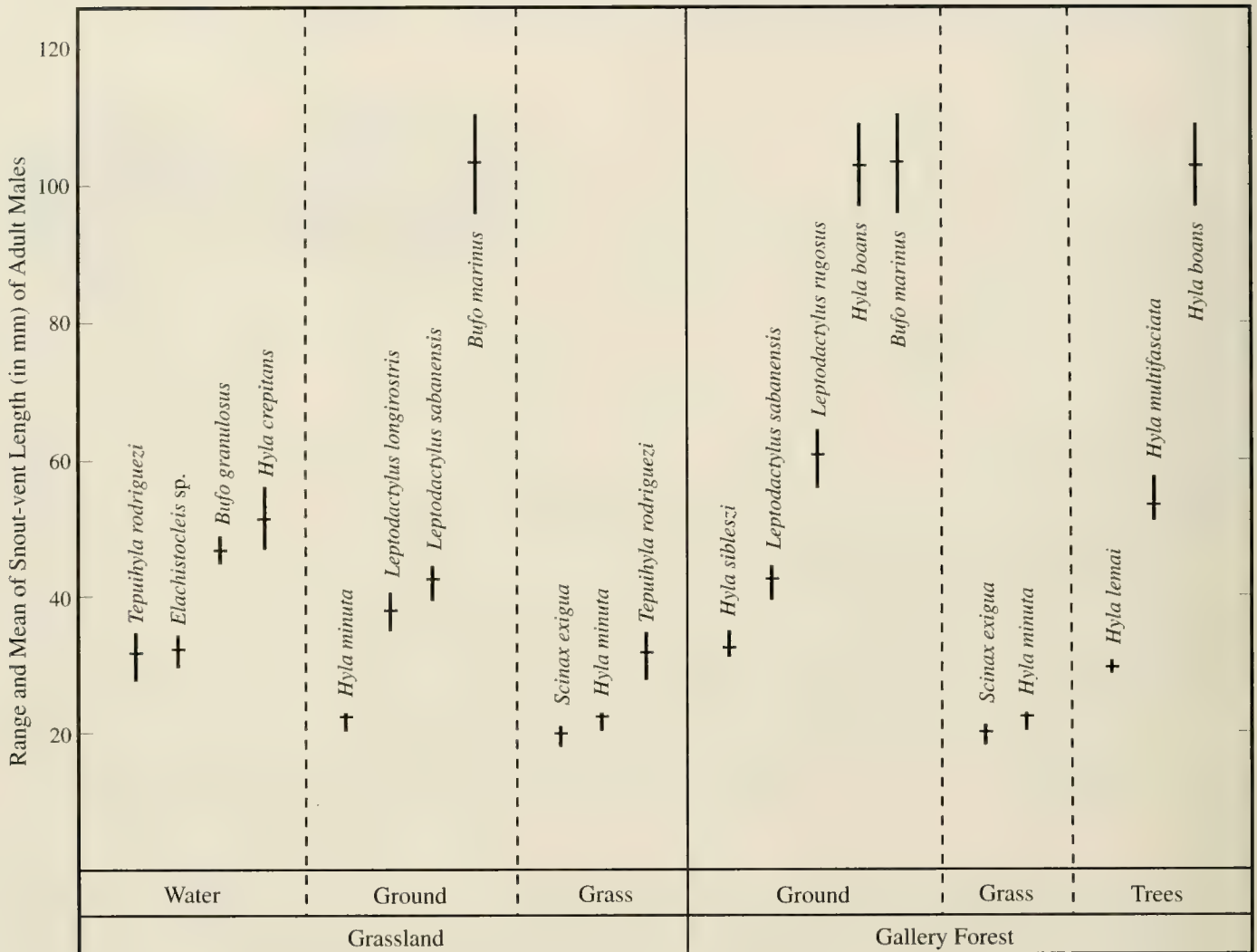


Fig. 33. Snout-vent lengths of adult males of 14 species of anurans with respect to perching and calling sites in grassland at Km 144 and in gallery forest at Cabanayén on the Gran Sabana, Estado Bolívar, Venezuela. Vertical bars = range; horizontal lines = mean.

species of *Leptodactylus* that occur in the very humid lower montane forest and on the Gran Sabana call from the ground in both habitats. However, a shift in microhabitat utilization seems to exist among a few species. *Hyla minuta* occurs throughout the region and usually calls from bushes and herbaceous plants, but in the grassland on the Gran Sabana, they call from the ground at the edge of, and emergent grasses in, temporary ponds. In the very humid lower montane forest, *Hyla lemai* and *Hyla sibleszi* call from bushes and herbaceous plants over streams, but in gallery forest on the Gran Sabana, the former was found in a tree, and the latter was on rocks at the edge of a stream.

In many cases, calling sites are correlated with oviposition sites, which in part reflect sites of development of the eggs and tadpoles. Reproductive mode is a combination of ovipositional and developmental factors; Duellman and Trueb (1986) defined 29 reproductive modes in

anurans. Twelve of these are found among anurans in the region under study (Table 7). Herein, one of the modes, arboreal eggs that hatch into tadpoles that drop into ponds or streams, is divided into those in which tadpoles develop in ponds (*Phyllomedusa*) and those in which tadpoles develop in streams (centrolenids and *Hyla lemai*). Although in each type of vegetation, the mode of eggs and tadpoles in lentic water is the most common (26.3% in very humid lower montane forest to 70.0% in grasslands on the Gran Sabana), the diversity of reproductive modes varies between different habitats. Only two modes (eggs and tadpoles in lentic water, and foam nest and feeding tadpoles in ponds) are found in all four habitats. The greatest number of modes (10) is found in the very humid lower montane forest, and the fewest (4) is in the grasslands on the Gran Sabana. Four modes (all involving terrestrial eggs or direct development) are restricted to the very humid lower

montane forest, and two modes involving foam nests are restricted to the humid tropical forest, whereas no modes are restricted to the Gran Sabana.

Lynch (1979) and Duellman and Trueb (1986) distinguished between forest and nonforest reproductive modes. In forest modes, the eggs (and in some cases the tadpoles) are exposed to air as they develop on the ground, on vegetation, or on the female; thus, egg development is dependent upon high atmospheric humidity. Five reproductive modes in the region are forest modes; these are the two modes with arboreal eggs, the two modes with terrestrial eggs, and the mode of eggs on the dorsum of an arboreal female. These modes occur in 11.1% of the species in the gallery forest on the Gran Sabana, in 13.5% of the species in the humid tropical forest, and in 42.1% of the species in the very humid lower montane forest; they are absent on the Gran Sabana. Even the high percentage of forest modes in the very humid lower montane forest is lower than the 61–92% (\bar{x} = 76.4) reported for five South American cloud forests (Duellman, 1988)⁵. This lower percentage is owing to the presence of species, such as *Hyla minuta* and *Pipa arrabali*, that breed in ponds created by road construction.

These limited data reveal distinct differences among anuran communities in different types of vegetation. The richest community in the humid tropical forest has nearly twice the number of species than do communities in the very humid lower montane forest, species of which make up most of the species composition in the gallery forest on the Gran Sabana. The depauperate community of anurans in the grasslands of the Gran Sabana includes nonarboreal species that also occur in the other areas, plus one species (*Elachistocleis* sp.) not known in the other habitats.

BIOGEOGRAPHIC ANALYSIS

DISTRIBUTION ALONG THE ELEVATIONAL GRADIENT

The transect from the lowland humid tropical forest from El Dorado to Las Claritas through the very humid lower montane forest on the slopes of the Sierra de Lema to the grasslands on the Gran Sabana provides an opportunity to examine distributions of anurans in diverse habitats along this elevational gradient. For purposes of comparison, data from the lowland savanna at El Manteco to the north of El Dorado (Hoogmoed and Gorzula, 1979) are included.⁶

A total of 64 species is known from this transect (Fig. 2, Table 8). Of the 26 species at El Manteco, five (*Scinax*

Table 7. Distribution of anuran reproductive modes (numbered as proposed by Duellman and Trueb, 1986) in major vegetation types. GS(G) = Gran Sabana (grassland), GS(GF) = Gran Sabana (gallery forest), HTF = humid tropical forest, VHLMF = very humid lower montane forest. Numbers in columns are numbers of species.

| Reproductive mode | HTF | VHLMF | GS(G) | GS(GF) |
|--|-----|-------|-------|--------|
| 1 Eggs and feeding tadpoles in lentic water | 22 | 5 | 7 | 4 |
| 2 Eggs and feeding tadpoles in lotic water | 0 | 2 | 1 | 1 |
| 3 Eggs and early tadpoles in basin-like nest | 1 | 1 | 0 | 1 |
| 8 Foam nest and feeding tadpoles in pond | 8 | 2 | 2 | 1 |
| 9 Foam nest and feeding tadpoles in stream | 0 | 1 | 1 | 1 |
| 21 Foam nest in burrow; tadpoles in pond | 1 | 0 | 0 | 0 |
| 22 Foam nest in burrow; direct development | 1 | 0 | 0 | 0 |
| 18a Eggs arboreal; tadpoles in pond | 4 | 0 | 0 | 0 |
| 18b Eggs arboreal; tadpoles in stream | 0 | 4 | 0 | 1 |
| 14 Eggs terrestrial; tadpoles carried to water | 1 | 1 | 0 | 0 |
| 17 Eggs terrestrial; direct development | 0 | 2 | 0 | 0 |
| 11 Eggs on dorsum of aquatic female; direct development | 0 | 1 | 0 | 0 |
| 27 Eggs on dorsum of arboreal female; direct development | 0 | 1 | 0 | 0 |

trilineata, *Leptodactylus macrosternum*, *L. pallidirostris*, *Physalaemus cuvieri*, *Elachistocleis ovalis*, and *Pseudis paradoxa*) are unknown elsewhere along the transect. Seventeen of the species at El Manteco are among the 36 species known from sites in the humid tropical forest (El Dorado, 13 km S Río Cuyuni, and Km 38–88 in Table 8). Some of these (e.g., *Bufo granulosus* and *Leptodactylus fuscus*) are typical savanna-inhabiting frogs that, as “weed” species, have invaded disturbed situations in humid tropical forest; several others (e.g., *Hyla geographica* and *Rana palmipes*) usually inhabit the lowland forests and apparently invade the gallery forests in the savanna at El Manteco. The rest of the shared species are frogs that are widely distributed in forests and savannas; some of these (e.g., *Bufo marinus* and *Scinax rubra*) are “weed” species that thrive in disturbed habitats and also occur in undisturbed humid tropical forest.

⁶ Subsequently *Hyla minuta* and *Physalaemus cuvieri* were collected at El Manteco by Stefan Gorzula (in litt.), who noted that the *Leptodactylus rugosus* reported by Hoogmoed and Gorzula (1979) was collected from a granitic area deep within the forest and has never been found on the savanna. The list of species in Table 8 and the Appendix have been modified accordingly.

⁵ Stefan Gorzula (in litt., 26 March 1996) noted that based on physico-chemical data from about 100 localities in the Venezuelan Guayana, there seems to be a good correlation between reproductive mode and water chemistry: “In areas where the available water is highly oligotrophic the species tend to be the ones with large eggs and direct development. As you go into more eutrophic habitats, the opportunistic anuran species laying a large number of small eggs and having free-living larvae become the norm.” To date, no analyses of water chemistry and anuran reproductive modes has been undertaken, but there exists a relationship between hydrochemical characteristics of habitats and the species of crocodylians that occur therein (Gorzula et al., 1988).

Table 8. Reported occurrence of species of anurans at 10 sites in Estado Bolívar, Venezuela.

| Species | El Manteco | El Dorado | Km 13 | Km 38–88 | Km 104 | Km 112–114 | Km 117–120 | Km 127 | Km 144 | Cabanayén |
|---------------------------------------|------------|-----------|-------|----------|--------|------------|------------|--------|--------|-----------|
| <i>Allophryne ruthveni</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Bufo granulosus</i> | + | + | + | – | – | – | – | – | + | + |
| <i>Bufo guttatus</i> | + | – | – | – | – | + | – | – | – | – |
| <i>Bufo marinus</i> | + | – | – | + | – | – | – | – | + | + |
| <i>Bufo nasicus</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Centrolene</i> sp. | – | – | – | – | – | – | – | + | – | – |
| <i>Hyalinobatrachium orientale</i> | – | – | – | – | – | + | + | – | – | – |
| <i>Hyalinobatrachium</i> sp. | – | – | – | – | – | – | + | – | – | – |
| <i>Colostethus parkerae</i> | – | – | – | – | – | + | + | – | – | – |
| <i>Dendrobates leucomelas</i> | + | – | – | – | + | – | – | – | – | – |
| <i>Epipedobates femoralis</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Hyla boans</i> | – | – | + | + | – | + | – | + | – | + |
| <i>Hyla crepitans</i> | + | + | + | – | – | – | – | – | + | + |
| <i>Hyla geographica</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Hyla lemai</i> | – | – | – | – | – | + | + | – | – | + |
| <i>Hyla microcephala</i> | + | + | + | + | – | – | – | – | – | – |
| <i>Hyla minuscula</i> | + | + | + | + | – | – | – | – | – | – |
| <i>Hyla minuta</i> | + | + | + | + | + | + | + | + | + | + |
| <i>Hyla multifasciata</i> | + | – | – | – | – | + | – | – | – | + |
| <i>Hyla sibleszi</i> | – | – | – | – | – | – | + | + | – | + |
| <i>Osteocephalus taurinus</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Phrynohyas venulosa</i> | + | – | + | – | – | – | – | – | – | – |
| <i>Phyllomedusa bicolor</i> | – | – | + | + | – | – | – | – | – | – |
| <i>Phyllomedusa hypocondrialis</i> | + | + | + | + | – | – | – | – | – | – |
| <i>Phyllomedusa tarsius</i> | – | – | + | + | – | – | – | – | – | – |
| <i>Phyllomedusa tomopterna</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Scinax boesemani</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Scinax danae</i> | – | – | – | – | – | – | – | + | – | – |
| <i>Scinax exigua</i> | – | – | – | – | – | – | – | – | + | + |
| <i>Scinax nebulosa</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Scinax rostrata</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Scinax rubra</i> | + | + | + | + | – | – | – | – | – | – |
| <i>Scinax trilineata</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Scinax x-signata</i> | + | + | + | – | – | – | – | – | – | – |
| <i>Sphaenorhynchus lacteus</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Stefania evansi</i> | – | – | – | – | – | + | + | – | – | – |
| <i>Tepuihyla rodriguezi</i> | – | – | – | – | – | – | + | – | + | – |
| <i>Adelophryne gutturosa</i> | – | – | – | – | – | – | + | – | – | – |
| <i>Adenomera hylaedactyls</i> | + | – | + | – | + | – | – | – | – | – |
| <i>Eleutherodactylus pulvinatus</i> | – | – | – | – | – | – | + | + | – | – |
| <i>Leptodactylus bolivianus</i> | + | – | + | + | + | – | – | – | – | – |
| <i>Leptodactylus fuscus</i> | + | – | + | – | – | – | – | – | – | – |
| <i>Leptodactylus leptodactyloides</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Leptodactylus longirostris</i> | – | – | – | – | + | + | + | + | + | + |
| <i>Leptodactylus macrosternum</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Leptodactylus mystaceus</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Leptodactylus pallidirostris</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Leptodactylus pentadactylus</i> | – | – | + | + | – | – | – | – | – | – |
| <i>Leptodactylus petersii</i> | – | – | – | + | – | – | – | – | – | – |
| <i>Leptodactylus rugosus</i> | – | – | – | – | + | + | – | + | – | + |
| <i>Leptodactylus sabanensis</i> | – | – | – | – | – | – | + | + | + | + |
| <i>Physalaemus cuvieri</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Physalaemus enesefae</i> | + | + | + | + | – | – | – | – | – | – |
| <i>Physalaemus pustulosus</i> | + | – | + | – | – | – | – | – | – | – |
| <i>Pleurodema brachyops</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Ctenophryne geayi</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Elachistocleis bicolor</i> | – | – | + | – | – | – | – | – | – | – |
| <i>Elachistocleis ovalis</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Elachistocleis</i> sp. | – | – | – | – | – | – | – | – | + | – |
| <i>Otophryne robusta</i> | – | – | – | – | – | – | + | – | – | – |
| <i>Pipa arrabali</i> | – | – | – | – | – | + | – | – | – | – |
| <i>Pseudis paradoxa</i> | + | – | – | – | – | – | – | – | – | – |
| <i>Rana palmipes</i> | + | – | – | + | – | – | – | – | – | – |

Among the 36 species known from the humid tropical forest, three (*Hyla minuta*, *Adenomera hylaedactyla*, and *Leptodactylus bolivianus*) are known from Km 104 on the lower (450 m) slopes of the Sierra de Lema, which supports lower premontane rainforest. Presumably, *Hyla boans* also occurs there, because that species and *Hyla minuta* are known from the very humid lower montane forest at higher elevations in the Sierra de Lema.

Of the 20 species recorded from the very humid lower montane forest at elevations of 860–1250 m (Km 112–114, Km 117–120, Km 127 in Table 8), 10 are unknown elsewhere along the transect, and five of these (*Centrolene* sp., *Hyalinobatrachium* sp., *Colostethus* 175986). Likewise, *Dendrobates leucomelas*, which occurs in gallery forest at El Manteco (Hoogmoed and Gorzula, 1979), was recorded at Km 104; it certainly occurs in the forests between El Dorado and Las Claritas. *Hyla multifasciata* is known from gallery forests at El Manteco and on the Gran Sabana and from one site on the slopes of the Sierra de Lema. Based on the broad distribution of this species, it most likely occurs at other sites along the transect. *Leptodactylus rugosus* is a habitat specialist (granitic domes) that is widely distributed in the Sierra de Lema and Gran Sabana (Heyer, 1995); it also occurs on a granitic dome at El Manteco (Hoogmoed and Gorzula, 1979). Its apparent absence in the forests between El Dorado and Las Claritas possibly is a result of the fact that no granitic domes were sampled in that area.

Hyla minuta is known from all of the sites and, thus, has the widest distribution along the transect. Eleven species (*Centrolene* sp., *Hyalinobatrachium* sp., *Colostethus parkerae*, *Hyla lemai*, *H. sibleszi*, *Scinax danae*, *S. exigua*, *Tepuihyla rodriguezi*, *Eleutherodactylus pulvinatus*, *Leptodactylus sabanensis*, and *Elachistocleis* sp.) are endemic to the highland region encompassing the Sierra de Lema and the Gran Sabana.⁷

DISTRIBUTION PATTERNS IN NORTHEASTERN SOUTH AMERICA

Northeastern South America contains an environmental mosaic of savannas and lowland tropical rainforests with a region of isolated tablelands at higher elevations, the tepuis, constituting the Guiana Highlands. This entire northeastern part of South America has been defined as the Guianan Region by Hoogmoed (1979b). The region is bordered on the north by the Río Orinoco, on the east by the Atlantic Ocean, on the south by the Río Amazonas and Río Negro, and on the west by the Río Negro and Río Orinoco (Fig. 34). Thus, the Guianan region encompasses southeastern Venezuela (the Venezuelan Guayana), Brazil north of the Río Amazonas west to the Río Negro, and all of Guyana, Suriname, and French Guiana. Geologically,



Fig. 34. Map of northeastern South America showing the Guianan Region (enclosed in dashed line) as defined by Hoogmoed (1979b).

this region represents most of the Guiana Shield, as defined by Gansser (1954) and Fittkau (1974). Although alluvial deposits exist along narrow fringes, especially to the north and south, most of the region has a core of pre-Cambrian metamorphic and igneous rocks, which have been emergent since the Paleozoic. The elevated tablelands are erosional remnants of Proterozoic sandstone (Roraima Formation) that was elevated in the Late Cretaceous (Priem et al., 1973; Haffer, 1974). Throughout the Guianan region, most soils are sandy alluvium resulting from erosion of the uplifted Roraima Formation. The rivers contain little sediment but have a high tannin content; thus, they are referred to as “black-water” rivers.

Since Hoogmoed's (1979b) biogeographic analysis of the herpetofauna of the Guianan Region, many new distributional data have become available, including those reported herein. The following analysis includes data (updated taxonomically) from six sites in savannas, five in lowland tropical rainforest, and one in montane cloud forest (Fig. 35). The sites in savanna are: Hato “El Guanote” (= La Guanota), Estado Apure, and Hato Masaguaral, Estado Guárico, Venezuela (Staton and Dixon, 1977); El Manteco, Estado Bolívar, Venezuela, Sipalwini and Zanderij, Surinam (Hoogmoed and Gorzula, 1979); and the Gran Sabana reported herein. In addition to the site 13 km S, 1 km E of the Río Cuyuni bridge reported herein, the sites in lowland tropical rainforest are: Petit Saut, French Guiana (Hoogmoed and Avila-Pires, 1991); upper Riviere Oyapock, French Guiana (Lescure, 1976); and the INPA-WWF Reserves about 80 km N of Manaus, Estado Amazonas, Brazil (Zimmerman and Rodrigues, 1990), plus one site barely peripheral to the Guianan region—Belém, Brazil (Crump, 1971). The sole cloud forest area is the north slope of the Sierra de Lema, Estado Bolívar, Venezuela, reported herein.

A total of 122 species of anurans has been recorded at the 12 sites; no more than 44 are known to occur at any

⁷ Stefan Gorzula (in litt., 26 March 1996) noted *Eleutherodactylus pulvinatus* from localities in montane forest up to 125 km airline from La Escalera. He also reported three additional localities for *Scinax exigua* in Estado Bolívar, Venezuela: Kanagapi Kapu (04°58' N, 61°13' W, 800 m), Mapauri savannas (04°56' W, 61°06' W, 900 m), and Piedra del Supamo (06°43' N, 62°31' W, 650 m).

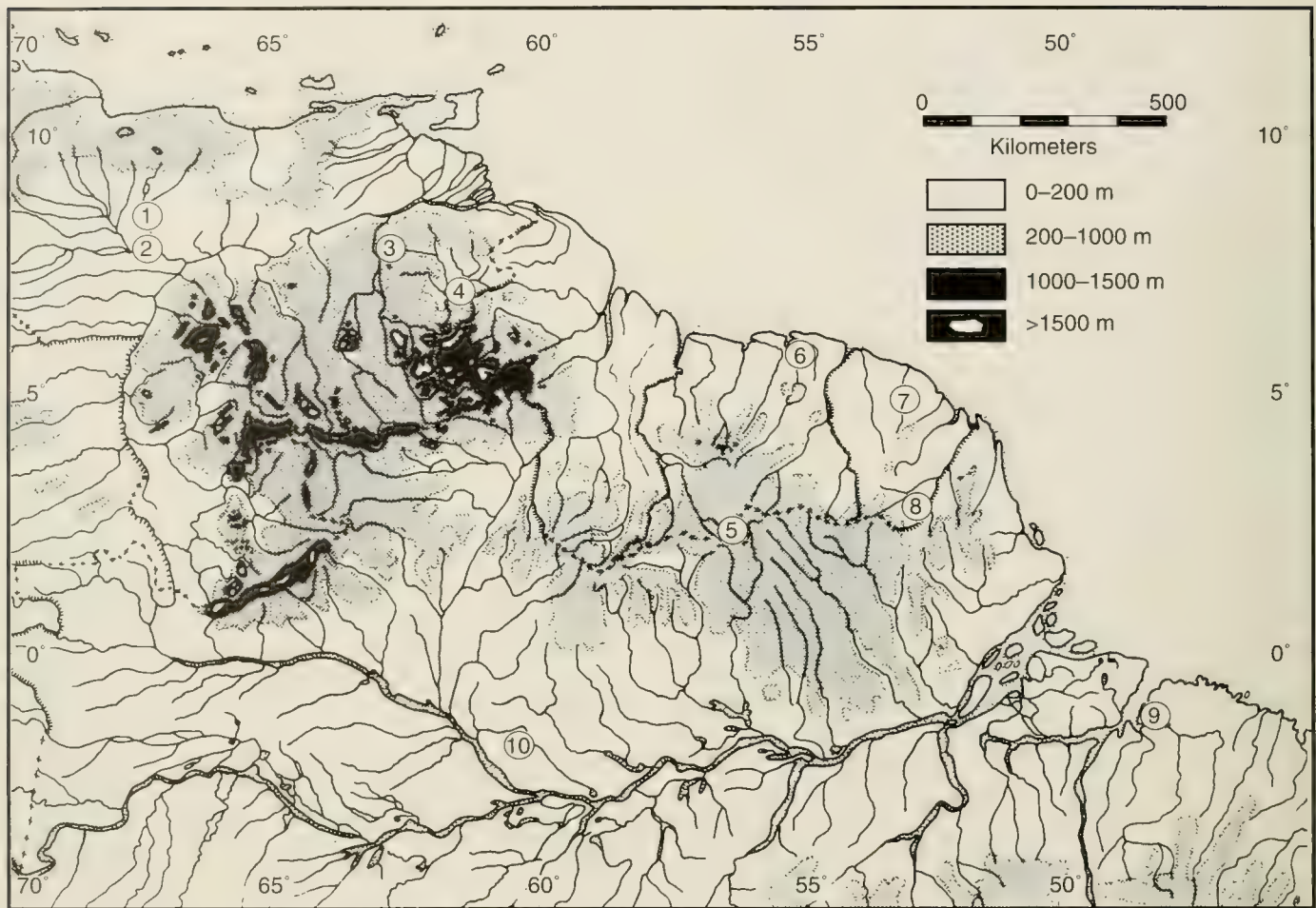


Fig. 35. Map of northeastern South America showing principal physiographic features. Numbers in circles are locations of sites used in biogeographic comparisons: 1 = Hato Masaguaral, Estado Guárico, Venezuela (savanna); 2 = Hato La Guanota, Estado Apure, Venezuela (savanna); 3 = El Manteco, Estado Bolívar, Venezuela (savanna); 4 = Río Cuyuni, Estado Bolívar, Venezuela (forest); 5 = Sipalwini, Suriname (savanna); 6 = Zanderij, Suriname (savanna); 7 = Petit Saut, French Guiana (forest); 8 = Upper Riviere Oyapock, French Guiana (forest); 9 = Belém, Estado Pará, Brazil; 10 = INPA-WWF Reserves north of Manaus, Estado Amazonas, Brazil. For location of sites in La Escalera region, including Sierra de Lema and La Gran Sabana, see figure 1. Modified from Hoogmoed (1979b:fig. 10.5).

one site (Appendix). Each species is known only from an average of 2.59 of the 12 sites; 49 (40.2%) of the species are known from only one of the sites. One species (*Bufo marinus*) is known from nine sites, and three species (*Hyla boans*, *Scinax rubra*, and *Leptodactylus fuscus*) are known from eight sites. These numbers and the following analysis should be viewed as minimal numbers and relationships. More intensive collecting at many of the sites, especially those in forests, probably will reveal additional species.

Hoogmoed (1979b) compared anuran faunas in lowland forests and in savannas in the Guianan Region. He noted that among forest-inhabiting anurans there is a distinctly higher resemblance between the anuran faunas of eastern Guiana (Guyana east of the Essequibo River, Suriname, French Guiana, and the northern part of Amapá, Brazil) than between both of those areas and western Guiana (Guyana west of the Essequibo River and Venezu-

elan Guayana). On the other hand, among savanna-inhabiting anurans, the resemblance between eastern Guiana and the Brazilian part of Guiana is only slightly higher than that between both of those areas and western Guiana. For the entire herpetofauna of the Guianan Region, Hoogmoed (1979b:264) concluded: "Within the area, the Essequibo-Rio Branco Depression forms a barrier for the distribution of a number of eastern forest species to the west and of western species to the east. No such function is present for savanna inhabitants that, with the exception of local endemics, are spread throughout the area."

Faunal resemblance among 12 sites in the Guianan Region was determined by calculating the coefficient of biogeographic resemblance (CBR) by the formula $2C/(N_1 + N_2) = \text{CBR}$, where C = number of species in common to Sites 1 and 2, N_1 = number of species at Site 1, and N_2 = number of species at Site 2 (Duellman, 1990). These calculations reveal that the number of species shared by any

Table 9. Occurrence of species of anurans at 12 sites in northeastern South America. (See Appendix.) Abbreviations in headings to columns correspond to sites in first column. See text and Figure 34 for locations of sites. The number of species at each site is shown in boldface in the common cell; the numbers of species that are shared by two sites are shown in the upper right, and the coefficients of biogeographic resemblance are in italics in the lower left.

| Site | MAS | GUA | EM | ZAN | SIP | GS | SL | CUY | PS | OYA | BEL | MAN |
|------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-----------|
| Masaguaral (MAS) | 16 | 15 | 15 | 8 | 5 | 3 | 1 | 9 | 3 | 2 | 4 | 2 |
| La Guanota (GUA) | <i>0.97</i> | 15 | 14 | 8 | 5 | 3 | 1 | 8 | 3 | 2 | 4 | 2 |
| El Manteco (EM) | <i>0.68</i> | <i>0.64</i> | 28 | 10 | 9 | 5 | 5 | 15 | 6 | 6 | 10 | 4 |
| Zanderij (ZAN) | <i>0.44</i> | <i>0.46</i> | <i>0.42</i> | 20 | 10 | 6 | 4 | 13 | 11 | 8 | 11 | 7 |
| Sipalwini (SIP) | <i>0.32</i> | <i>0.33</i> | <i>0.42</i> | <i>0.51</i> | 15 | 4 | 4 | 7 | 5 | 3 | 5 | 3 |
| Gran Sabana (GS) | <i>0.19</i> | <i>0.20</i> | <i>0.23</i> | <i>0.34</i> | <i>0.27</i> | 15 | 9 | 6 | 5 | 2 | 2 | 3 |
| Sa. de Lema (SL) | <i>0.05</i> | <i>0.05</i> | <i>0.19</i> | <i>0.18</i> | <i>0.21</i> | <i>0.46</i> | 24 | 4 | 4 | 4 | 2 | 4 |
| Cuyuni (CUY) | <i>0.36</i> | <i>0.33</i> | <i>0.48</i> | <i>0.48</i> | <i>0.29</i> | <i>0.31</i> | <i>0.14</i> | 34 | 13 | 15 | 16 | 16 |
| Petit Saut (PS) | <i>0.12</i> | <i>0.12</i> | <i>0.19</i> | <i>0.39</i> | <i>0.20</i> | <i>0.22</i> | <i>0.13</i> | <i>0.37</i> | 36 | 18 | 12 | 16 |
| Oyapock (OYA) | <i>0.07</i> | <i>0.08</i> | <i>0.18</i> | <i>0.28</i> | <i>0.11</i> | <i>0.08</i> | <i>0.13</i> | <i>0.42</i> | <i>0.49</i> | 38 | 18 | 20 |
| Belém (BEL) | <i>0.15</i> | <i>0.15</i> | <i>0.31</i> | <i>0.39</i> | <i>0.19</i> | <i>0.08</i> | <i>0.07</i> | <i>0.45</i> | <i>0.33</i> | <i>0.48</i> | 37 | 12 |
| Manaus (MAN) | <i>0.07</i> | <i>0.07</i> | <i>0.11</i> | <i>0.23</i> | <i>0.11</i> | <i>0.10</i> | <i>0.12</i> | <i>0.42</i> | <i>0.41</i> | <i>0.50</i> | <i>0.30</i> | 42 |

two sites ranges from one (savanna at Masaguaral and cloud forest in the Sierra de Lema, and savanna at La Guanota and cloud forest in the Sierra de Lema) to 20 (rainforests at Oyapock and Manaus). The CBRs range from 0.05 between those two savannas and the Sierra de Lema to 0.97 between Masaguaral and La Guanota (Table 9). Savannas in the lowlands to the west of the Essequibo River–Rio Branco Depression (Masaguaral, Guanote, El Manteco) have CBRs of 0.64–0.97 ($\bar{x} = 0.76$, $n = 3$), and the CBR between two savannas east of the depression (Zanderij and Sipalwini) is 0.51, whereas the CBRs between the western and eastern savannas in the lowlands are 0.32–0.46 ($\bar{x} = 0.40$, $n = 6$). Thus, there are greater faunal differences between eastern and western savannas in the lowlands than among savannas in either region. The Gran Sabana at an elevation in excess of 1200 m is in the Venezuelan Guayana west of the Essequibo River–Rio Branco Depression, but its anuran fauna is more like those in eastern savannas in the lowlands than those in western savannas in the lowlands; the range of CBRs between the Gran Sabana and three western savannas is 0.19–0.23 ($\bar{x} = 0.21$) and between the Gran Sabana and two eastern savannas, 0.27–0.34 ($\bar{x} = 0.31$).

Two sites (Cuyuni and Manaus) in lowland rainforest to the west of the Essequibo River–Rio Branco depression have a CBR of 0.42, and three sites (Petit Saut, Oyapock, and Belém) to the east of the depression have CBRs of 0.33–0.49 ($\bar{x} = 0.43$), whereas CBRs between the western and eastern sites in lowland rainforest are 0.30–0.50 ($\bar{x} = 0.41$), only slightly less than among sites to the east or west of the depression.

When anuran faunas in lowland savannas and rainforests are combined, a slightly different pattern emerges. Among five sites to the west of the Essequibo River–Rio Branco Depression, CBRs are 0.07–0.97 ($\bar{x} = 0.42$), and among five sites to the east of the depression, the CBRs are more alike but the mean is lower, 0.19–0.49 ($\bar{x} = 0.32$). The much higher CBR for among sites to the west of the depression is owing to the fact that 15 of the 16 species at

Masaguaral also occur at La Guanota and have a CBR of 0.97. By eliminating this combination, the CBRs in the lowlands to the west of the depression are 0.07–0.71 ($\bar{x} = 0.36$). Comparison of all lowland sites to the east with those to the west of the depression reveals CBRs of 0.07–0.53 ($\bar{x} = 0.28$). The combination of habitats shows a slightly lower faunal resemblance across the Essequibo River–Rio Branco Depression than among sites on either side of the depression, but when the closely approximated savannas at Masaguaral and Guanote are treated as one, the difference essentially disappears.

As has been pointed out above, faunal similarity is lower between the Gran Sabana and other savannas west of the Essequibo River–Rio Branco Depression than between the Gran Sabana and the savannas to the east of the depression. However, the opposite is true in comparison of the Gran Sabana with lowland rainforests; the CBRs between the Gran Sabana and two sites (Cuyuni and Manaus) in western rainforests are slightly higher, 0.10–0.31 ($\bar{x} = 0.21$), than three sites (Petit Saut, Oyapock, and Belém) in eastern rainforests, 0.08–0.22 ($\bar{x} = 0.13$). The Gran Sabana has its greatest faunal similarity with cloud forests on the adjacent Sierra de Lema; the CBR is 0.46. Nine of the 16 species known from the Gran Sabana are among the 24 species known from cloud forests on the Sierra de Lema. The similarity between the cloud forests on the Sierra de Lema and all sites other than the Gran Sabana is low. The CBRs with other habitats and regions are: western rainforests, 0.12–0.14 ($\bar{x} = 0.13$, $n = 2$); eastern rainforests, 0.07–0.13 ($\bar{x} = 0.11$, $n = 3$); western savannas, 0.05–0.19 ($\bar{x} = 0.10$, $n = 3$); eastern savannas, 0.18–0.21 ($\bar{x} = 0.20$, $n = 2$).

The site at the Río Cuyuni has an interesting combination of forest-inhabiting species (e.g., *Epipedobates femoralis*, *Hyla boans*, *H. granosa*, *Osteocephalus taurinus*, *Phyllomedusa bicolor*, and *Adenomera hylaedactyla*) and species (e.g., *Bufo granulosus*, *Hyla crepitans*, *Hyla microcephala*, *Leptodactylus fuscus*, and *Physalaemus pustulosus*) that are usually found in savannas but in disturbed (e.g., edge of road) areas at

Table 10. Comparisons of anuran faunas within and between habitats. Means are in parentheses below ranges. CBR = Coefficient of biogeographic resemblance; n = number of comparisons.

| Habitat | n | Distance (Km) | Total species | Species in common | CBR |
|---|-----|-------------------|-----------------|-------------------|---------------------|
| Savannas (all) | 6 | 24–659 (375) | 15–26 (17.8) | 3–15 (8.0) | 0.19–0.97 (0.43) |
| Savannas (minus Gran Sabana) | 5 | 24–659 (408) | 15–26 (18.4) | 5–15 (9.9) | 0.32–0.97 (0.53) |
| Rainforests (all) | 5 | 126–790 (473) | 34–42 (37.4) | 12–20 (15.6) | 0.30–0.50 (0.42) |
| Rainforests (minus Belém & Manaus) | 3 | 126–470 (338) | 34–38 (36.0) | 13–18 (15.3) | 0.37–0.49 (0.43) |
| Savannas–rainforests | 30 | 100–1094 (534) | 15–42 (26.6) | 2–14 (5.6) | 0.07–0.48 (0.20) |
| Savannas (all)–cloud forest | 6 | 16–338 (255) | 15–24 (18.6) | 1–9 (4.8) | 0.05–0.46 (0.19) |
| Savannas (minus Gran Sabana)–cloud forest | 5 | 214–338 (303) | 15–24 (19.0) | 1–5 (3.0) | 0.05–0.21 (0.14) |
| Rainforests–cloud forest | 5 | 83–772 (439) | 24–42 (35.2) | 2–4 (2.8) | 0.07–0.14 (11.8) |

the Río Cuyuni. Furthermore, the faunal similarities are nearly equal between the site at the Río Cuyuni and other sites in lowland rainforest and those in savannas; the CBRs with other sites are: western forests, 0.42 (Manaus), eastern forests, 0.37–0.45 (\bar{x} = 0.41, n = 3); western savannas, 0.33–0.48 (\bar{x} = 0.39, n = 3); eastern savannas, 0.29–0.53 (\bar{x} = 0.41, n = 2).

Comparison of anuran faunas at particular sites, instead of general patterns of distribution as done by Hoogmoed (1979b) provides slightly different results—essentially no greater differences between sites in lowland rainforest to the east and west of the Essequibo River–Rio Branco Depression than among sites on either side of the depression, but distinctly greater differences between sites in lowland savannas to the east and west of the depression than among sites on either side of the depression. The latter pattern exists in a less noticeable form when habitats are ignored. However, the anuran faunas on the Gran Sabana and in the cloud forest on the northern slopes of the Sierra de Lema are distinctive and more alike than either is to faunas in the savannas and rainforests in the lowlands. All of these data, together with distances separating sites, are summarized in Table 10.

Distance between sites might be a factor in determining faunal similarity. Two close sites (24 km between savannas at Masaguaral and La Guanota) have the highest CBR (0.97). The two closest sites (16 km between grassland on the Gran Sabana and cloud forest on the north slopes of the Sierra de Lema) have a CBR of 0.46, but this is much lower than the CBRs between El Manteco and Masaguaral (0.71) and La Guanota (0.68), separated by 256 and 259 km, respectively.

Duellman and Thomas (1996) showed a significant negative correlation to exist between distance and species of anurans shared by nine sites in rainforest in the upper Amazon Basin. Plotting of CBRs against distances between

12 sites in northeastern South America reveals great scattering of data points (Fig. 36). Correlation analyses of all sites and by habitat revealed significant negative correlations ($P < 0.01$) between distances and CBRs among sites in savannas, between sites in savannas and lowland rainforest, and between sites in savannas and cloud forest. All other correlations were not significant.

Hoogmoed (1979b) placed biogeographic emphasis on a wide zone of lower rainfall extending northwest–southeast from the llanos of Venezuela to the caatinga and cerrados of Brazil and including the inland savannas in the lowlands of the Guianas. Haffer (1969; 1974; 1979) and others have proposed that during glacial epochs of the Pleistocene, rainfall was lowered in the tropical lowlands and that savannas replaced much of the rainforest. If this hypothesis is correct, existing savannas in the lowlands are remnants of former widespread, continuous grasslands. Furthermore, dry periods have been identified in the Quaternary; the last of these was 3500–2800 years before present (Haffer, 1979). Thus, possibly much of the lowland rainforest in northeastern South America may have existed for less than 3000 years. The seasonality and relatively low amount of rainfall may be responsible for the depauperate anuran fauna in northeastern South America as contrasted to that in the upper Amazon Basin of Ecuador and northern Peru, where rainfall is higher and distributed throughout the year. A significant positive correlation exists between rainfall and species richness from Ecuador to Bolivia in the upper Amazon Basin (Duellman and Thomas, 1996).

The foregoing analysis of distribution patterns of anurans in northeastern South America reveals rather consistent data on distributions within savannas. However, the anuran faunas in the lowland rainforests may not be so well known; they certainly are depauperate compared to nine sites in the upper Amazon Basin having 40–84 (\bar{x} =

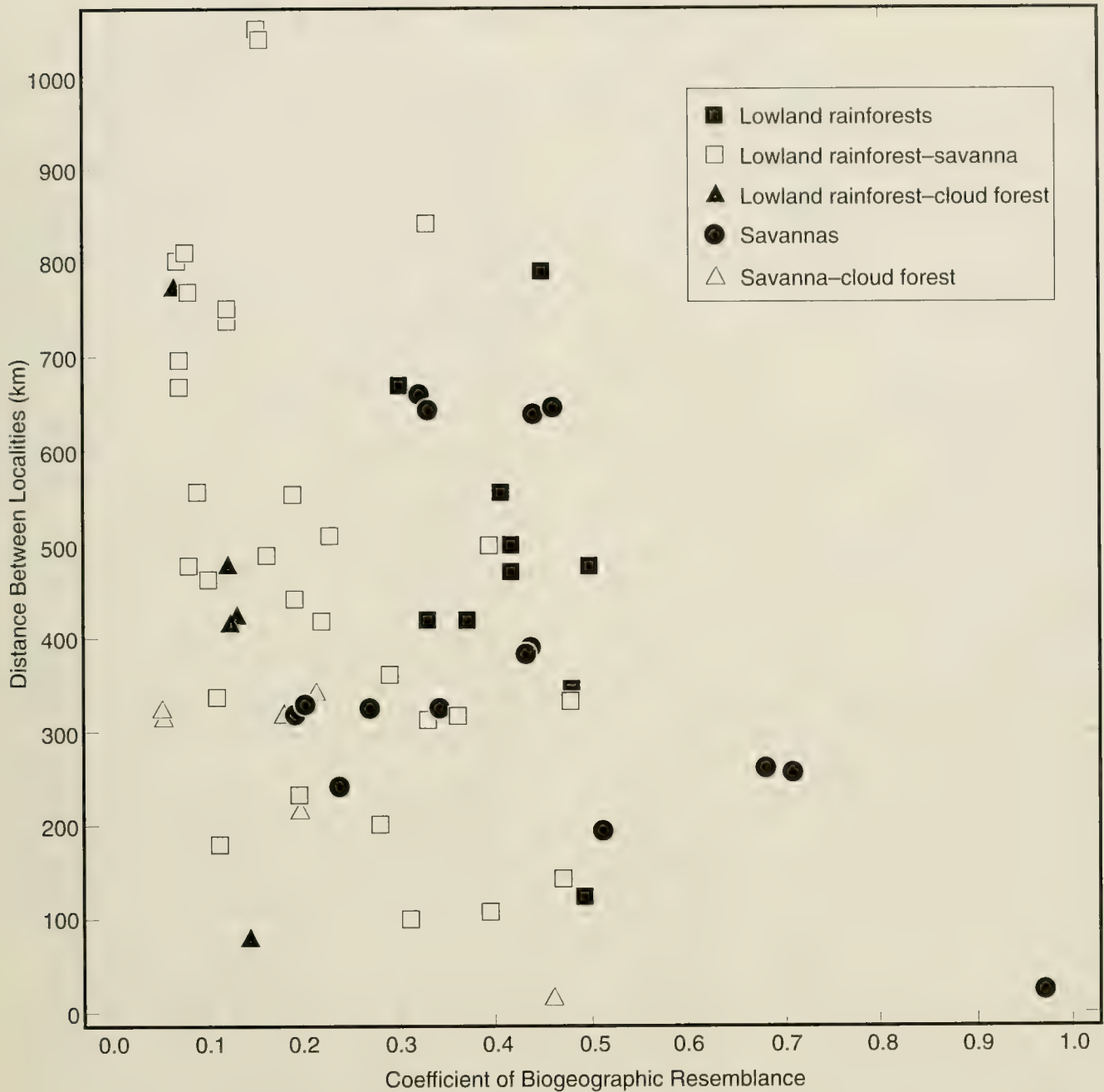


Fig. 36. Relationships between distances among 12 sites in northeastern South America and coefficients of biogeographic resemblance among anurans at those sites.

61.8) species (Duellman and Thomas, 1996). The anuran fauna (24 species) in the cloud forest on the northern slopes of the Sierra de Lema is not depauperate in comparison with cloud forests in the Andes, which have 20–39 ($\bar{x} = 25.4$, $n = 5$) species (Duellman, 1988). However, the composition of the faunas differs. In the Andes about 50% of the anuran fauna is composed of *Eleutherodactylus* at any given site in cloud forests, whereas only one species of *Eleutherodactylus* is known from the Sierra de Lema, the fauna of which is rich in *Leptodactylus* and *Hyla*.

A comprehensive understanding of the anuran fauna of northeastern South America will require thorough sampling of more sites in the lowlands, in the cloud forests on the slopes of the highlands, and on the southern part of the Gran Sabana. The cloud forests and the Gran Sabana have been largely neglected. The international expeditions to the tepuys (Donnelly and Myers, 1991; Myers and Donnelly, 1996, 1997; Zweifel, 1986) will add an important dimension to the interpretation of the origin of the highland herpetofauna.

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APPENDIX

Occurrence of species of anurans at 12 sites in northeastern South America. Abbreviations for names of sites are: BEL = Belém, Estado Pará, Brazil; CUY = Rio Cuyuni and lowlands to south, Estado Bolívar, Venezuela; EM = El Manteco, Estado Bolívar, Venezuela; GS = Gran Sabana, Estado Bolívar, Venezuela; GUA = Hato La Guanota, Estado Apure, Venezuela; MAN = INPA-WWF Reserves, N of Manaus, Estado Amazonas, Brazil; MAS = Hato Masaguaral, Estado Guárico, Venezuela; OYA = Upper Riviere Oyapock, French Guiana; P S = Petit Saut, French Guiana; SIP = Sipalwini, Suriname; S L = Sierra de Lema, Estado Bolívar, Venezuela; ZAN = Zanderij, Surinam. CF = cloud forest; + = present; - = not known to occur.

| SPECIES | SAVANNA | | | | | | C F | RAINFOREST | | | | |
|------------------------------------|---------|-----|----|-----|-----|----|-----|------------|-----|-----|-----|-----|
| | MAS | GUA | EM | ZAN | SIP | GS | S L | CUY | P S | OYA | BEL | MAN |
| ALLOPHRYNIDAE: | | | | | | | | | | | | |
| <i>Allophryne ruthveni</i> | - | - | - | - | - | - | - | + | - | + | - | - |
| BUFONIDAE: | | | | | | | | | | | | |
| <i>Atelopus franciscus</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Atelopus pulcher</i> | - | - | - | - | - | - | - | - | - | + | - | + |
| <i>Bufo dapsilis</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Bufo granulosus</i> | + | + | + | + | - | + | - | + | - | - | - | + |
| <i>Bufo guttatus</i> | - | - | + | - | - | - | + | - | + | + | - | - |
| <i>Bufo marinus</i> | + | + | + | + | + | + | - | - | + | + | + | - |
| <i>Bufo nasicus</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Bufo "typhonius"</i> | - | - | - | - | - | - | - | - | + | + | + | - |
| <i>Dendrophryniscus minutus</i> | - | - | - | - | - | - | - | - | - | + | - | + |
| CENTROLENIDAE: | | | | | | | | | | | | |
| <i>Centrolene</i> sp. | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Cochranella oyampiensis</i> | - | - | - | - | - | - | - | - | + | + | - | + |
| <i>Hyalinobatrachium orientale</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Hyalinobatrachium taylori</i> | - | - | - | - | - | - | - | - | + | + | - | - |
| <i>Hyalinobatrachium</i> sp. | - | - | - | - | - | - | + | - | - | - | - | - |
| DENDROBATIDAE: | | | | | | | | | | | | |
| <i>Colostethus beebei</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Colostethus brunneus</i> | - | - | - | - | - | - | - | - | - | + | - | + |
| <i>Colostethus degranvillei</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Colostethus parkerae</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Colostethus stepheni</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Dendrobates leucomelas</i> | - | - | + | - | - | - | + | - | - | - | - | - |
| <i>Dendrobates quinquevittatus</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| <i>Dendrobates tinctorius</i> | - | - | - | - | - | - | - | - | - | + | - | - |
| <i>Epipedobates femoralis</i> | - | - | - | - | - | - | - | + | + | + | - | + |
| <i>Epipedobates trivittatus</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| HYLIDAE: | | | | | | | | | | | | |
| <i>Hyla boans</i> | - | - | - | + | + | + | + | + | + | + | - | + |
| <i>Hyla brevifrons</i> | - | - | - | - | - | - | - | - | - | + | + | + |
| <i>Hyla calcarata</i> | - | - | - | - | - | - | - | - | - | + | + | - |
| <i>Hyla crepitans</i> | + | + | + | + | - | + | - | + | - | - | - | - |
| <i>Hyla fasciata</i> | - | - | - | - | - | - | - | - | + | + | - | - |
| <i>Hyla geographica</i> | - | - | + | - | + | - | - | + | - | + | + | + |
| <i>Hyla granosa</i> | - | - | - | - | - | - | - | + | - | + | + | + |
| <i>Hyla lemai</i> | - | - | - | - | - | + | + | - | - | - | - | - |
| <i>Hyla leucophyllata</i> | - | - | - | + | - | - | - | - | + | + | + | - |
| <i>Hyla melanargyrea</i> | - | - | - | + | - | - | - | - | + | - | + | - |
| <i>Hyla microcephala</i> | + | + | + | - | - | - | - | + | - | - | + | - |
| <i>Hyla minuscula</i> | - | - | + | - | - | - | - | + | - | + | + | - |
| <i>Hyla minuta</i> | - | - | + | - | - | + | + | + | + | - | + | + |
| <i>Hyla multifasciata</i> | - | - | + | + | + | + | + | - | - | - | + | - |
| <i>Hyla ornatissima</i> | - | - | - | - | - | - | - | - | - | + | - | - |
| <i>Hyla raniceps</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| <i>Hyla sibleszi</i> | - | - | - | - | - | + | + | - | - | - | - | - |
| <i>Hyla</i> sp. | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Osteocephalus buckleyi</i> | - | - | - | - | - | - | - | - | - | + | - | + |
| <i>Osteocephalus leprieurii</i> | - | - | - | - | - | - | - | - | - | + | - | - |
| <i>Osteocephalus oophagus</i> | - | - | - | - | - | - | - | - | + | - | - | + |
| <i>Osteocephalus taurinus</i> | - | - | - | + | - | - | - | + | + | + | + | + |
| <i>Phrynohyas coriacea</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Phrynohyas resinifictrix</i> | - | - | - | - | - | - | - | - | - | + | + | + |
| <i>Phrynohyas venulosa</i> | + | + | + | - | - | - | - | + | - | - | + | - |
| <i>Phyllomedusa bicolor</i> | - | - | - | + | - | - | - | + | + | + | + | + |
| <i>Phyllomedusa hypocondrialis</i> | - | - | + | + | + | - | - | + | - | - | + | - |
| <i>Phyllomedusa tarsius</i> | - | - | - | - | - | - | - | + | - | - | - | + |

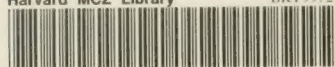
APPENDIX (Continued)

| SPECIES | SAVANNA | | | | | | C F | | RAINFOREST | | | |
|---------------------------------------|---------|-----|----|-----|-----|----|-----|-----|------------|-----|-----|----|
| | MAS | GUA | EM | ZAN | SIP | GS | S L | CUY | P S | OYA | BEL | MA |
| <i>Phyllomedusa tomodon</i> | - | - | - | - | - | - | - | + | + | + | - | + |
| <i>Phyllomedusa vaillanti</i> | - | - | - | - | - | - | - | - | + | - | + | + |
| <i>Scinax boesemani</i> | - | - | - | + | - | + | - | + | + | - | + | - |
| <i>Scinax cruentomma</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Scinax danae</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Scinax exigua</i> | - | - | - | - | - | + | - | - | - | - | - | - |
| <i>Scinax nebulosa</i> | - | - | - | + | + | - | - | + | - | - | + | - |
| <i>Scinax parkeri</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Scinax proboscidea</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Scinax rostrata</i> | - | - | - | - | - | - | - | + | - | - | - | - |
| <i>Scinax rubra</i> | + | + | + | + | - | - | - | + | + | + | + | - |
| <i>Scinax trilineata</i> | - | - | + | - | + | - | - | - | - | - | - | - |
| <i>Scinax s-signata</i> | - | - | + | + | + | - | - | + | + | - | - | - |
| <i>Scinax sp. A.</i> | - | - | - | - | + | - | - | - | + | - | - | - |
| <i>Scinax sp. B</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| <i>Sphaenorhynchus lacteus</i> | - | - | + | - | - | - | - | + | - | - | + | - |
| <i>Stefania evansi</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Tepuihyla rodriguezi</i> | - | - | - | - | - | + | + | - | - | - | - | - |
| LEPTODACTYLIDAE: | | | | | | | | | | | | |
| <i>Adelophryne gutturosa</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Adenomera hylaedactyla</i> | - | - | - | + | - | - | + | + | + | + | - | + |
| <i>Adenomera marmorata</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| <i>Ceratophrys cornuta</i> | - | - | - | - | - | - | - | - | - | + | - | + |
| <i>Eleutherodactylus chiasonotus</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Eleutherodactylus fenestratus</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Eleutherodactylus inguinalis</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Eleutherodactylus lacrimosus</i> | - | - | - | - | - | - | - | - | - | + | + | - |
| <i>Eleutherodactylus marmoratus</i> | - | - | - | - | - | - | - | - | - | - | - | - |
| <i>Eleutherodactylus ockendeni</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Eleutherodactylus pluvius</i> | - | - | - | - | - | - | + | - | - | - | - | - |
| <i>Eleutherodactylus zeuctotylus</i> | - | - | - | - | - | - | - | - | + | - | - | - |
| <i>Eleutherodactylus zimmermanae</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Leptodactylus bolivianus</i> | + | + | + | + | + | - | + | + | - | - | - | - |
| <i>Leptodactylus fuscus</i> | + | + | + | + | + | - | - | + | + | - | - | + |
| <i>Leptodactylus knudseni</i> | - | - | - | - | - | - | - | - | + | - | - | + |
| <i>Leptodactylus labialis</i> | + | + | - | - | - | - | - | - | - | - | - | - |
| <i>Leptodactylus leptodactyloides</i> | - | - | - | - | - | - | - | + | - | - | - | - |
| <i>Leptodactylus longirostris</i> | - | - | - | - | + | + | + | - | - | - | - | - |
| <i>Leptodactylus macrosternum</i> | + | + | + | - | + | - | - | - | - | - | - | - |
| <i>Leptodactylus mystaceus</i> | - | - | - | - | - | - | - | + | + | + | + | + |
| <i>Leptodactylus ocellatus</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| <i>Leptodactylus pallidirostris</i> | + | + | + | + | + | - | - | - | - | - | - | - |
| <i>Leptodactylus pentadactylus</i> | - | - | - | + | - | - | - | + | - | + | + | + |
| <i>Leptodactylus petersii</i> | - | - | - | - | - | - | - | + | + | + | + | + |
| <i>Leptodactylus rhodomystax</i> | - | - | - | - | - | - | - | - | + | + | + | + |
| <i>Leptodactylus riveroi</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Leptodactylus rugosus</i> | - | - | - | - | - | + | + | - | - | - | - | - |
| <i>Leptodactylus sabanensis</i> | - | - | - | - | - | + | + | - | - | - | - | + |
| <i>Leptodactylus stenodema</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Lithodytes lineatus</i> | - | - | - | - | - | - | - | - | - | - | - | - |
| <i>Physalaemus enesefae</i> | + | - | + | - | - | - | - | + | - | - | - | - |
| <i>Physalaemus ephippifer</i> | - | - | - | - | - | - | - | - | - | - | + | - |
| <i>Physalaemus petersi</i> | - | - | - | - | - | - | - | - | - | + | + | - |
| <i>Physalaemus pustulosus</i> | + | + | + | - | - | - | - | + | - | - | - | - |
| <i>Pleurodema brachyops</i> | + | + | + | - | - | - | - | - | - | - | - | - |
| <i>Pseudopaludicola pusilla</i> | - | - | - | - | + | - | - | - | - | - | - | - |
| MICROHYLIDAE: | | | | | | | | | | | | |
| <i>Chiasmocleis shudikarensis</i> | - | - | - | - | - | - | - | - | + | - | - | + |
| <i>Chiasmocleis sp.</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Ctenophryne geayi</i> | - | - | - | - | - | - | - | + | - | - | - | + |
| <i>Elachistocleis bicolor</i> | - | - | - | - | - | - | - | + | - | - | - | - |
| <i>Elachistocleis ovalis</i> | + | + | + | + | - | - | - | - | - | - | - | - |
| <i>Elachistocleis sp.</i> | - | - | - | - | - | + | - | - | - | - | - | - |
| <i>Hamptophryne boliviana</i> | - | - | - | - | - | - | - | - | + | - | - | - |

APPENDIX (Continued)

| SPECIES | SAVANNA | | | | | | C F | | RAINFOREST | | | |
|-------------------------------------|---------|-----|----|-----|-----|----|-----|-----|------------|-----|-----|----|
| | MAS | GUA | EM | ZAN | SIP | GS | S L | CUY | P S | OYA | BEL | MA |
| <i>Otophryne robusta</i> | - | - | - | - | - | - | + | - | - | + | - | - |
| <i>Synapturanus mirandaribeiroi</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| <i>Synapturanus salseri</i> | - | - | - | - | - | - | - | - | - | - | - | + |
| PIPIDAE: | | | | | | | | | | | | |
| <i>Pipa arrabali</i> | - | - | - | - | - | - | + | - | - | - | - | + |
| <i>Pipa pipa</i> | - | - | - | - | - | - | - | - | - | + | + | - |
| PSEUDIDAE: | | | | | | | | | | | | |
| <i>Pseudis paradoxa</i> | + | + | + | - | - | - | - | - | - | - | - | - |
| RANIDAE: | | | | | | | | | | | | |
| <i>Rana palmipes</i> | - | - | + | - | - | - | - | + | - | + | - | - |

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